1983

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Iowa State University PH.D. 1983

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by

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A Dissertation Submitted to the
Graduate Faculty in Partial Fulfillment of the
Requirements for the Degree of
DOCTOR OF PHILOSOPHY

Department: Agronomy
Major: Plant Breeding and Cytogenetics

Approved:

Signature was redacted for privacy.

In Charge of Major Work

Signature was redacted for privacy.

For the Major Department

Signature was redacted for privacy.

For the Graduate College

Iowa State University
Ames, Iowa

1983

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INTRODUCTION

Grain sorghum [*Sorghum bicolor* (L.) Moench] breeders have two major concerns regarding diversity. First, they are acutely aware that all commercial grain sorghum hybrids are produced presently by using the A_1 milo-kafir cytoplasmic-genetic male sterility system, with the result that all commercial hybrids possess a singular cytoplasm. Steps are being taken to incorporate different cytoplasms to broaden the cytoplasm base. Secondly, breeders are aware and concerned that too few lines are being used as seed and pollen parents of hybrids, and that the nuclear base of sorghum hybrids also lacks breadth.

One potential avenue for surmounting the second concern is to create diverse sorghum random-mating populations which may prove useful for inbred line development. Because sorghum is largely (ca. 94%) self-pollinated, it was necessary to introduce genes for male sterility into the populations so that outcrossing could be fostered. The development of Iowa population number 1, restorer in A_1 cytoplasm and undergoing mass selection [IAP1R(M)], was begun in 1973 at Ames, Iowa. It possessed the ms_3 allele for genetic male sterility. The lines used to develop IAP1R all restored pollen fertility completely when used in crosses to A-lines possessing the A_1 milo cytoplasm. About 80% of the germplasm used in developing IAP1R was adapted for production in the United States, while 20% consisted of converted exotic sorghums.

The purpose of my research was to evaluate the breeding potential of IAP1R after three cycles of gridded mass selection. Population means and variances were estimated for grain yield, the primary components of

yield, and other agronomic traits. Additionally, estimates were obtained for the heritability of these traits, phenotypic and genetic correlations among them, expected gains from selection with different recurrent selection procedures, and correlated responses to selection.

LITERATURE REVIEW

A recent survey of the grain sorghum [Sorghum bicolor (L.) Moench] germplasm base in the United States (Harvey, 1977) revealed that private companies in the hybrid seed industry were using only 35 public inbred lines. These public inbreds were used as females in 87% and as males in 69% of the production fields reported. One public seed parent, Wheatland, accounted for 45% of the reported acreage. Another public line (Tx 2536) and its two backcross derivatives, were used as the male parent in 55% of the reported acreage. Both public and private breeders are acutely aware of the need to diversify the germplasm base. The survey showed that a majority of the private breeders preferred that public agencies develop and release germplasm in the form of populations improved by recurrent selection.

Development of Sorghum Random-Mating Populations

Grain sorghums are predominantly (ca. 94%) self-pollinated (Poehlman, 1979). Therefore, random mating is not possible on a practical scale without the incorporation of cytoplasmic-genetic or genetic male sterility. The world's first sorghum random-mating population, NP1BR, was synthesized in 1960 by O. J. Webster in Nebraska (Nordquist et al., 1973). This population was constituted by intermating A, B, and R-lines using the cytoplasmic-genetic male-sterile (ms_c) A-lines as females. Random mating or planned crosses were made by using the male-sterile segregates each generation. The world's second and third random-mating sorghum populations were synthesized in the early 1960s by Jowett (1965)

at Serere, Uganda. Jowett also used the milo-kafir A_1 cytoplasm system of male sterility, ms_c, as described by Stephens and Holland (1954). The populations were difficult to propagate under Ugandan conditions because of an extremely low percentage of completely male-sterile segregates and poor pollen shed caused by a preponderance of partial sterility in the fertile plants. Another disadvantage of all populations that used the ms_c type of sterility was that only R-lines (fertility restorer) could be developed from these populations.

A purely genetic type of male sterility had been noted in the variety Coes in 1940 at the Nebraska Agricultural Experiment Station (Webster, 1965). Webster showed that this male sterility was controlled by a single recessive gene, $\underline{ms}_3$, located on chromosome three. Plants homozygous recessive at this locus, $\underline{ms}_3\ \underline{ms}_3$, are completely female fertile, but their anthers produce no viable pollen. The nuclear gene operates independently of the cytoplasm, and the phenotype is stable over most environments. This male-sterility system has been used widely in populations for the development of R-lines, B-lines, or a mixture of the two. Several other nuclear genes conditioning male sterility have been reported, but only $\underline{ms}_3$, $\underline{ms}_7$, and $\underline{al}$ have been used widely (Ross et al., 1971). The $\underline{ms}_3$ gene was added to NP1BR in 1962 (Nordquist et al., 1973). All $\underline{ms}_3$ populations have the Coes cytoplasm unless the lines used to form a random-mating population are hand emasculated and used as the female parent during the incorporation of the $\underline{ms}_3$ gene. This has rarely been done, and there has been some concern among breeders about the lack of cytoplasmic diversity in sorghum random-mating populations (Ross et al., 1971).

Some sorghum breeders have been opposed to the incorporation of genetic male sterility into sorghum populations. Maunder (1972) questioned the desirability of incorporating such genes, based on advice he received from R. W. Allard. Allard believed that ample variability would be generated in populations under conditions of low to moderate outcrossing, and that too much outcrossing would tend to break up favorable linkages. Therefore, Maunder proposed that because most of the outcrossing in sorghum is concentrated in the upper one-third of the panicle (Maunder and Sharp, 1963), one could achieve a degree of random mating by simply harvesting that portion of the panicle of selected plants. Selections from such populations do not require purification for fertility. However, the degree of random mating in such a population would be several orders of magnitude below that of a population with genetic male sterility. Also, most sorghum breeders welcome a certain amount of segregation for male sterility in breeding lines since it facilitates crossing. The International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) has a policy of releasing breeding lines that still segregate for $\underline{ms}_3$ and $\underline{ms}_7$ to plant breeders, and sister lines purified for fertility to farmers (House, 1982).

Theoretical Aspects of Sorghum Random-Mating Populations

Random mating in sorghum populations over several generations by using genetic male sterility to enforce outcrossing is designed to promote recombination and insure the formation of a wide diversity of genotypes through the breakup of initial linkage blocks. Doggett (1970)

considered that frequent crossing among heterozygotes was essential to break up tight repulsion-phase linkages and thereby release hidden variability. Doggett (1972) enumerated several reasons why recurrent selection in a sorghum random-mating population should be superior to pedigree selection for a quantitative trait such as yield. First, not enough crosses are made in the pedigree system to break up linkage groups, and the rapid achievement of homozygosity through selfing minimizes the probability of effective crossing over. Second, in pedigree selection the population size required to recover the desired genotype becomes impossible to grow when more than a few genes are involved. Third, only a small number of parents are used in pedigree selection, resulting in a lack of genetic diversity. In contrast, sorghum random-mating populations may contain a diversity of germplasm, the chances for breaking up linkages are optimized, and through recurrent selection the gene frequencies of favorable alleles are increased. Therefore, the probability of recovering the desired genotype from a population of limited size is improved greatly over time.

Hanson (1959) has shown theoretically that in a diploid species a minimum of four generations of random mating without selection should be employed to insure the breakup of initial linkage blocks before beginning selection. In practice, most sorghum breeders grow random-mated populations for only three generations before beginning selection, and at times some mild selection has been imposed during this period (Eberhart, 1970; Doggett, 1972; Gardner, 1972; Nordquist et al., 1973; Ross, 1973).

The choice of parental materials to use in compositing a population

will depend on the breeder's goals. Eberhart (1970) reported that participants in the Sorghum Workshop Conference in Puerto Rico proposed four basic types of populations. Type I populations would be control populations made up from only superior U. S. germplasm. Type II populations would be made up of elite germplasm collected worldwide. Type III populations would be made up from agronomically elite materials which had a high frequency of genes confering resistance to specific diseases or insects. Type IV populations would be germplasm pools which were intended to provide germplasm for long range goals.

Theoretical considerations lead Gilmore (1964) to propose that male sterility, genetic or cytoplasmic-genetic, should be incorporated into populations of autogamous species that may be wind-pollinated, such as sorghum. He proposed that reciprocal recurrent selection should be used in these random-mating populations in order to capitalize on all types of gene action, as suggested by Comstock et al. (1949). However, Doggett (1970) questioned the value of reciprocal recurrent selection in sorghum based on studies which showed that gene action was primarily additive.

A comprehensive breeding system, with recurrent selection in random-mating populations as its keystone, was applied to maize (Zea mays L.) breeding at Kitale, Kenya (Eberhart et al., 1967). A variety of population improvement methods were tested. Populations improved by recurrent selection were expected to be sources of improved population crosses, variety hybrids, synthetics, and hybrids. As a result of associations and discussions with Eberhart, Doggett became convinced of the efficiency of the comprehensive breeding system, and Doggett and Eberhart (1967)

described the use of this system for sorghum. They proposed that the testing of S_1 lines would be the most efficient method for sorghum population improvement in Uganda because (1) it required no bagging of heads or manual crossing (2) great variability for yield and other quantitative traits was expressed among S_1 progenies (3) one cycle of three generations could be completed in one year at Serere, Uganda (4) there would be ample opportunities to apply stringent selection for agronomic traits during the selection of parental S_0 plants and in the recombination planting (5) S_2 lines could be extracted each cycle by selecting the very best fertile plants in the recombination block. They suggested that sorghum random-mating populations should be composited in such a way as to exploit heterotic patterns and on the basis of classification as fertility restoring (R-lines) or non-fertility restoring (B-lines).

The $\underline{ms}_3$ gene has been used to develop sorghum populations with a mixture of local and exotic germplasm with a minimum of effort on the part of the breeder. Doggett and Majisu (1967) outlined a program for incorporating $\underline{ms}_3$ into promising world-collection lines so that this "museum" could become a useful source of genetic variability for long term breeding goals. Each promising line was crossed to A, Redlan to determine if it was a fertility restorer or a non-restorer. Based on fertility classification, the lines then were crossed onto male-sterile segregates of the appropriate population. A similar system was described by Singh (1977) for the development of cold-tolerant sorghums for the high altitude, arid areas of central Mexico.

Although a knowledge of gene action is helpful, recurrent selection

in a sorghum random-mating population will result in gradual improvement if selection is effective regardless of the genes involved, their number, their location on the chromosome, or their effect on plant metabolism (Gardner, 1972). Choice of the breeding method appropriate for a particular random-mating population will be dictated by the breeder's goals, the operational resources required for each method, and expected gains from selection for each method. Estimates of additive and dominance genetic variances, heritabilities, and genetic correlations are invaluable in predicting genetic gain. Empig et al. (1972) presented formulae for calculating expected gains from selection using different recurrent selection methods that are specifically applicable to maize, but may be applied to other crops such as sorghum. Based on the ratio of additive genetic variance to number of generations per cycle, they proposed that the most efficient intrapopulation methods were (1) mass selection with control of both parents (2) mass selection with control of one parent (3) modified ear-to-row testing and (4) S_1 testing. Reciprocal full-sib selection was judged the most efficient interpopulation improvement method.

Doggett (1968) advocated mass selection (recurrent phenotypic selection) mainly for highly heritable traits, but also for yield when used with isolations divided into grids as proposed by Gardner (1969). Doggett showed with sorghum that predicted gains would double if control of both parents was obtained. Such control is easy to obtain for a trait identifiable before anthesis, but for a trait such as yield it can only be obtained by harvesting fertile selfed plants. Therefore, Doggett

proposed a system with sorghum of alternating selection in which fertile plants are selected one generation, followed by a generation of recombination in which male-steriles are selected.

Gardner (1972) believed that mass selection, S_1 selection, and full-sib selection were the most promising methods for population improvement in sorghum. S_1 or S_2 selection for lowly-heritable traits and mass selection for traits with higher heritabilities was favored by Eberhart (1972). Ross (1973) outlined the operational aspects of several population improvement procedures for sorghum. He pointed out that S_1 testing is especially effective because it is operationally simple (requires no crossing or bagging), allows complete parental control, and yield tests are conducted only every third generation. Full-sib testing, however, requires much laborious hand crossing and as many or more yield tests as are needed with S_1 testing.

A theoretical approach involving genetic modeling and Monte Carlo simulations was used by Wright (1980) to show that S_1 testing was preferable to all other methods evaluated (half-sib, testcross, and mass selection) for intrapopulation improvement when heritability of the traits under selection was below the critical value of about 0.38. Sprague and Eberhart (1976) have shown that S_2 testing may provide gains per unit of time that are equal to those for S_1 testing. Additionally, there is the advantage of having only one yield test every four generations and the opportunity for more rigorous selection for agronomic traits in the more highly inbred families.

Quantitative Genetic Studies in Sorghum Random-Mating Populations

Although there have been many studies on quantitative traits in sorghum, the germplasm base represented in each study was relatively narrow (Beil and Atkins, 1967; Collins and Pickett, 1972; Laosuwon and Atkins, 1977, 1978; Wilson et al., 1978). Quantitative genetic studies of type I and type II sorghum random-mating populations have been reported with NP3R at Nebraska and PP9 at Purdue, respectively (Jan-orn et al., 1976; Bittinger et al., 1981). Jan-orn tested 196 half-sib, full-sib, and S_1 families during one year at two Nebraska locations, while Bittinger evaluated 150 families in a Design I field experiment during two years at one Indiana location.

Estimates of additive variance were greater than those for dominance for all traits measured except grain yield and kernels/plant in NP3R, and grain yield in PP9. In NP3R, the S_1 family variance for yield was greater than the full-sib variance, which was greater than the half-sib variance. This S_1 variance, $\sigma^2_{A*} + 1/4\sigma^2_D$, was less than the estimate of σ^2_A for all traits studied in NP3R. σ^2_{A*} is equal to σ^2_A only when $p = q = 0.5$ or there is no dominance or epistasis. Estimates of σ^2_{A*} in relation to estimates of σ^2_A showed that σ^2_{A*} was not a good estimator of σ^2_A in NP3R. The ratio $\hat{\sigma}^2_{A*}/\hat{\sigma}^2_A$ for most traits was about 0.50. Jan-orn and Gardner interpreted this to suggest that the frequency of favorable alleles in NP3R was less than 0.50, and that dominance and even epistasis might have been important. They warned, however, that such interpretations are risky since there may have been a bias in estimating σ^2_A because very early and very late male-sterile plants may not have been

tagged. Also, they suggested that σ^2_D may have been underestimated. In PP9, low ratios of $\hat{\sigma}^2_D/\hat{\sigma}^2_A$ were interpreted as evidence that partial dominance was the main type of gene action for all traits studied except yield. The high ratio of $\hat{\sigma}^2_D/\hat{\sigma}^2_A$ for yield, 1.24, indicated that complete dominance or overdominance may have been important for this trait. However, the authors suggested that σ^2_D may have been underestimated because of assortative mating.

Estimates of heritabilities from broad-based, random-mating populations of sorghum are very useful in formulating the proper methods of selection to improve those populations for specific traits. In view of the diversity of germplasm in populations, it would appear that these estimates would have broader applicability than estimates derived from a narrow genetic base such as segregating generations from a cross of two inbred lines. Jan-orn et al. (1976) reported narrow-sense heritabilities based on individual-plant data in NP3R ranging from 0.09 for grain yield/unit area and 0.16 for heads/plant, to 0.88 for days to midbloom and 0.71 for plant height. Narrow-sense heritability values for kernel weight, 0.45, and kernels/head, 0.40 were intermediate in magnitude. Broad-sense heritabilities calculated on a family-mean basis in both NP3R and PP9 were much higher than individual plant heritabilities, but yield was again the least heritable trait, with days to midbloom and plant height the most heritable (Jan-orn et al., 1976; Bittinger et al., 1981).

Correlation studies in random-mating populations are interesting in view of the broad range of germplasm represented. Phenotypic correlations in NP3R between grain yield/unit area and both plant height and

days to midbloom were highly significant ($P < 0.01$) for all three family types (S_1, half-sib, full-sib), but coefficients of determination were less than 30% (Koraiem et al., 1979). Kernels/head and kernels/plant were the traits most highly correlated with grain yield/unit area in NP3R (with the exception of related traits such as yield/head and yield/plant), with coefficients of determination as large as 65%. Kernel size was not significantly correlated with grain yield. Grain yield per unit area in PP9 was significantly correlated only with days to midbloom, 0.48, and panicle weight, 0.70 (Bittinger et al., 1981). Genetic correlations in both NP3R and PP9 usually were larger than phenotypic correlations, but the relationships among traits remained constant (Koraiem et al., 1979; Bittinger et al., 1981). Eckebil et al. (1977) reported genetic correlations determined by using S_1 families selected from three Nebraska random-mating populations, NP3R, NP5R, and NP7BR. Genetic correlations among traits tended to be highest in NP5R (broad genetic base), intermediate in NP3R (intermediate genetic base), and lowest in NP7BR (narrow genetic base). Genetic correlations showed that grain yield/unit area was most highly correlated with yield/head and plant height (kernels/head was not considered in this study). Kernel size showed moderate to low correlation with grain yield. Days to midbloom was poorly and negatively correlated with yield, but this estimate was biased by the fact that many of the 200 random S_1 families tested per population were too late for Nebraska conditions.

Given a knowledge of means, variances, heritabilities, and genetic correlations among traits in a population, one may then calculate

expected gains from selection and correlated responses to selection. Jan-orn et al. (1976) determined that mass selection in NP3R would be preferable to family selection on a gain per generation basis only for the traits days to midbloom, plant height, and kernel size. Assuming three generations per cycle, S_1 family selection was the most effective method for improvement of grain yield, kernels/head, and kernels/plant. The expected gain per cycle for yield, when the highest yielding 10% of the S_1 families were recombined, was 9.3 q/ha (18%). Bittinger et al. (1981) predicted that recombination of the top 10% of the half-sib families in PP9 would result in a 5.6% gain in grain yield per cycle. Eckebil et al. (1977) showed that correlated responses to selection for grain yield alone in S_1 families of NP3R, NP5R, and NP7BR were mainly in favorable directions, although unfavorable large increases in plant height and a small decrease in percentage protein were predicted. Selection for large kernels in NP5R was estimated to result in 52% of the yield gain that would be attained by selection for grain yield alone. Bittinger et al. (1981) predicted that selection for grain yield alone in half-sib families of PP9 would result in unfavorable increases per cycle of 0.7 (29.4%) in lodging ratings, 19.9 cm (8.9%) in plant height, and 3.4 days (5.4%) in days to midbloom.

Evidence that major height genes have large pleiotropic effects on grain yield comes from studies with several sorghum populations (Doggett, 1972; Jan-orn et al., 1976; Bittinger et al., 1981), and from studies with isogenic lines (Casady, 1965; Graham and Lessman, 1966). The method of recurrent selection in random-mating populations, however, is

designed to act on the many minor genes or polygenes that affect yield, and thus should be effective even when height is restricted. Data from Nebraska (Ross, 1978), India (ICRISAT, 1977), and Nigeria (Obilana and El-Rouby, 1980) have supported this hypothesis, although it is evident that restrictions on height have slowed gains for grain yield.

Results of Selection in Random-Mating Populations

Mass selection has been used widely in random-mating populations. Mass selection for grain yield has been somewhat successful when selections were made in a gridded field to reduce environmental effects. Jan-orn (1975) visually selected the best fertile and male-sterile plants in each grid of 20 plants in an isolation planting of NP3R. A composite of seed from selected male-sterile plants was planted for recombination in the greenhouse where random mating produced seed for the C1 generation. Gains in grain yield over the base population were 295 g/plot (11.2%) for the progeny of selected fertile plants, 368.6 g/plot (14%) for the progeny of selected male-steriles, 180.4 g/plot (6.8% but not beyond $P < 0.05$) for the progeny of male-steriles from the recombination, and -274.5 g/plot (-10.4%) for the progeny of fertiles from the recombination. Gains in yield were accompanied by significant ($P < 0.05$) gains in kernels/plant, kernels/head, and kernel size. However, the C1 was eight days later and 23 cm taller than the base population.

Doggett (1972) tested gridded mass selection for grain yield in eight random-mating sorghum populations. An average of 40% of the male-sterile plants were selected each cycle to form the next generation.

Selection was practiced for three cycles or generations, and the average gain per generation was 1.4 q/ha (2.5%). Maturity did not change, but there was an average gain per generation for plant height of 12.7 cm (6%). Obilana and El-Rouby (1980) applied gridded mass selection to two Nigerian $\underline{ms}_7$ sorghum random-mating populations for three cycles. Each cycle the top 5% of the male-sterile plants were selected on the basis of head weights. Average gains per generation for head weight/plot were 0.73 kg (12.8%) for the B-population and 0.72 kg (13.5%) for the R-population. There were no significant ($P < 0.05$) maturity changes, but one population did have a significant ($P < 0.05$) increase in plant height.

Non-gridded mass selection in a foundation seed lot of Double Dwarf Yellow Milo 38 not segregating for male sterility was studied at Davis, California (Foster et al., 1980). Ten cycles of high and low selection for kernel size, plant height, and days to flower were completed. The outcrossing rate in this pure line variety was estimated at 16.5% in the sixth cycle, which is unusually high for grain sorghums. Realized heritabilities were very low, 0.09 to 0.14, for these traits, which usually show moderate to high heritability. This likely results from a lack of genetic diversity in this pure line variety. Mean per cycle gains ranged from 0.25% for early flowering to 3.4% for increased seed size.

Mass selection for the quantitative trait resistance to cold injury lead to the development of lines that set seed normally at altitudes up to 2350 m (7,710 ft.) in central Mexico where sorghum could not be grown previously (Livera and Carballo, 1976). Mass selection for sorghums

that were tolerant to acid soils in Georgia was successful and lead to the release of the acid soil tolerant germplasm population GP1R (Duncan, 1981).

Alternating mass selection in which fertile plants are selected one generation and male-steriles the next should be more effective than straight mass selection of male-steriles since there is complete parental control in half of each cycle. Doggett (1972) tried both methods in eight sorghum populations. Alternating selection resulted in about one and a half times the gain in grain yield, and better control of plant height. Ross et al. (1981) used the alternating method to select for high and low percentage protein in NP7BR. Fertile plants were selected in each grid, seed was evaluated in the laboratory, and the best 15% for high or low protein were planted in separate recombination blocks. Two cycles were completed in each direction. Changes per cycle for percentage protein were +0.3% and -0.35%, respectively. The sub-population selected for low protein significantly ($P < 0.05$) outyielded its high protein counterpart.

Complete parental control can be obtained when mass selection is practiced for a trait that is observable before anthesis. Mass selection with intermating of selected plants has been used successfully to select for resistance to diverse pests and diseases of sorghum (ICRISAT, 1978; Duncan et al., 1982; Webster and Schmalzel, 1978), cold tolerance (Mendoza et al., 1977), tolerance to high soil temperatures at germination (Scheuring et al., 1978), maximum subcrown internode elongation to allow deep planting to reach moisture under drought conditions (Scheuring

et al., 1978), and for improved forage quality in a sudangrass [Sorghum sudanense (Piper) Stapf] population (Gorz et al., 1982).

Mass selection with control of both parents also has been used effectively in tobacco. Tobacco, Nicotiana tabacum L., is an autogamous species that is easily emasculated and crossed. Matzinger et al. (1977) completed four cycles of gridded mass selection for harvestable leaf yield in which plants were selected before anthesis and paired crosses were made between selected plants. The average gain per cycle in harvestable leaf yield was 4.29%. The same technique was used for five cycles to select for reduced plant height and greater leaf number, and gains per cycle were 4.9% and 7%, respectively.

Recurrent selection based on half-sib family testing was reported for the maintainance and improvement of seven sorghum type IV populations at ICRISAT (ICRISAT, 1976). Ross (1978) reported the results of two cycles of half-sib family selection for grain yield in the sorghum population NP3R. The top 20% of the families were recombined each cycle, and each cycle required three generations. Realized gains over the C0 were 8.7 q/ha (21%) for the C1, and 5.5 q/ha (14%) for the C2. The C2 yield was lower than the C1 yield because stringent selection to keep plant height and maturity at desired levels in the C1 families which were recombined to form the C2 resulted in a lowered selection intensity for yield. The mean yield of the C2 was not significantly ($P < 0.05$) different from the yield of a commercial hybrid check, RS626. Estimated additive genetic variance was slightly greater in the C1 than in the C0.

Full-sib family selection has not been used extensively in sorghum

because of the considerable amount of time and labor involved in making the required crosses. This system was studied by Ross (1978), however, in an experiment in which three family selection methods (half-sib, full-sib, S_1) were compared in the population NP3R. Selection intensity was 20%, and three years were required for each cycle. For the full-sib method yield gains over the C0 were 7.5 q/ha (19%) for the C1, and 3.9 q/ha (10%) for the C2. The C2 yield was not significantly ($P < 0.05$) different from the yield of the hybrid RS626. The variance among full-sib families was less in the C1 than the C0, but this was believed to be a result of assortative mating which occurred because of intense selection for reduced height and earlier maturity.

S_1 family selection has been very popular in sorghum because it is operationally very simple and allows better control of agronomic traits such as plant height and maturity than is attainable with half-sib testing or mass selection. Doggett (1972) yield tested 334 S_1 lines from each of four populations, recombining the top 90 lines (27%) in each population. One cycle of three generations was completed. The average gain of the C1 over the C0 was 13.9 q/ha (25%), which is 8.3% per generation. The C1 of the best population was significantly ($P < 0.05$) higher in grain yield than the check varieties. However, average plant height in the C1 was 279 cm, 64 cm taller than the C0. Maturity of the C1 was within acceptable limits.

Scientists at ICRISAT (1977) evaluated the original and improved versions of eight sorghum populations. Two cycles of S_1 visual selection had been completed in four populations, and the average increase in

grain yield per cycle was 4.7 q/ha (13%). Plant height was reduced an average of 28 cm (11%) per cycle, to 196 cm. Two populations that were advanced through one cycle of S_1 yield testing gained an average of 2.1 q/ha (6%) for yield. Height was reduced 31 cm, to 176 cm. Two populations that were improved by one cycle of S_1 visual selection followed by one cycle of S_1 yield testing gained only 0.09 q/ha (0.25%) per cycle for grain yield. Height was reduced 13 cm (7%) per cycle, to 146 cm. Averaged over all eight populations, the yield gain was 2.9 q/ha (8.1%) per cycle of S_1 testing. It is remarkable that such a yield increase was achieved considering the strong selection pressures applied for reduced plant height, tan plant color, earlier maturity, and improved food quality grain.

Ross (1978) tested S_1 family selection in a study of selection methods in the sorghum population NP3R. Recombination of the highest yielding 20% of the S_1 families tested resulted in a yield gain over the C0 of 10.4 q/ha (26%) for the C1, and 6.9 q/ha (17%) for the C2. Lack of further gain in the C2 was attributed to strict selection for plant height and maturity. Mean grain yield of the C2 was not significantly ($P < 0.05$) different from the yield of the hybrid RS626. The S_1 family variance was somewhat lower in the C1 than the C0, probably because of intense selection for shorter and earlier S_1 families. The C0 mean plant height in NP3R was 124 cm, while the desired plant height for this population was 110-120 cm (Koraiem et al., 1979). Ross (1978) also completed two cycles of S_1 testing in the broad-based type II population NP5R, which has a high frequency of tall and late plants. The gain in

grain yield over the C0 was 0.6 q/ha (1%) for the C1, and there was no gain above the level of the C0 in the C2. Again, intense selection for reduced plant height and earlier maturity was practiced in each cycle. Still, the grain yield in C2 was not significantly ($P < 0.05$) different from the yield of a hybrid check, RS626.

Adequate sampling of parental S_0 fertile plants from a sorghum random-mating population is essential for maximum progress in S_1 family recurrent selection. The effect of genotype-environment interactions on sampling was studied by Ross and Hookstra (1983). They selected 200 random S_0 fertile plants from each of three yearly plantings of the same sorghum population (NP16BR), and then evaluated the S_1 progenies from the three samples. Differences in means, variances, estimated heritabilities, and estimated gains from selection were small and of little plant breeding importance. Therefore, they concluded that the environment at sampling did not significantly affect the likelihood of making plant breeding gains.

Recurrent selection using S_1 testing also has been applied successfully in breeding for disease and insect resistance in sorghums. Starks et al. (1976) used S_1 and half-sib families from the population KP2BR in screening for seedling resistance to biotype C of the greenbug, Schizaphis graminum (Rondani). Lines developed by population breeding were more resistant than lines developed by pedigree selection. The sorghum populations RP1R and RP2B, which have high yield potential and resistance to biotype C of the greenbug, were developed by using S_1 family recurrent selection (Ross et al., 1977). This selection method

also was used effectively to develop the Texas population TP18RB, a head smut resistance source population (Miller and Rosenow, 1978). S_1 testing under conditions of artificial infestations of the European corn borer [Ostrinia nubilalis (Hübner)] in RP2B and NP11BR resulted in increased levels of resistance in successive cycles, as measured by the percentage of S_1 lines that were classified as resistant (Atkins et al., 1983).

S_2 family recurrent selection has supplanted S_1 testing in advanced breeding populations at ICRISAT (House, 1982). Sorghum populations under S_2 testing have been improved 8% to 15% per cycle for grain yield. Advanced-cycle population bulks and population crosses both outyielded the hybrid check in one study at ICRISAT.

Utilization of Superior Lines Developed Through Population Breeding

The maxim that improved lines can be isolated from improved populations (Eberhart, 1972; Ross, 1980) has proved true for sorghum random-mated populations. Scientists at ICRISAT, under the leadership of Dr. Hugh Doggett until 1976, have used population breeding extensively since the center was established in 1973 (ICRISAT, 1974). By 1977 lines derived from improved populations were surpassing hybrid checks in grain yield, and one population-derived line, Fast Lane R-53, ranked first in the 1977 International Sorghum Yield Trial (ICRISAT, 1978). House (1982) reported that as many excellent lines were coming from the population breeding program as from pedigree selection. He also reported that one population-derived line, Melkamash, had been released to farmers in Ethiopia. Bhola Nath, the ICRISAT sorghum breeder who devotes

100% of his efforts to population breeding, reported (1982) that at least four other lines besides Melkamash that were derived from early cycles of the population breeding program, were likely to be released. Improved populations are expected to be increasing useful sources of new lines. Empirical evidence for this theoretical expectation was provided in a study of random lines drawn from the C0, C1, C2, and C3 of the US/R population. When equal numbers of random S_1 lines from each cycle were yield tested, it was found that of the highest yielding 10% of all S_1 lines tested, none came from the C0 or C1, the C2 contributed 25% and the C3 75%.

Otte and Ross (1981) tested the combining ability of R-lines derived from NP3R after three cycles of random mating. Twenty population-derived R-lines and 10 component R-lines of NP3R adapted to Nebraska conditions were crossed onto the same two A-lines. The hybrids of the population-derived lines had significantly ($P < 0.01$) higher grain yields than the hybrids of the component lines. Greenbug resistant lines developed from KP2BR have proved useful as male parents of hybrids (Starks et al., 1976). Type III random-mating populations, developed for resistance to a specific pest or disease, have yielded useful parental lines. For example, the Texas Experiment Station has released seven midge [Contarinia sorghicola (Coquillett)] resistant germplasm lines derived from TP6B and TP8R (Johnson et al., 1982).

Interest in population development for breeding and genetic studies, as well as for the selection of improved lines, has increased markedly in the past decade. The Texas Agriculture Experiment Station

alone has 28 sorghum random-mating populations in various stages of development (F. Miller, Texas A & M University, College Station, Texas, sorghum random-mating populations under development, personal communication, 1982). Sorghum breeders at experiment stations in Nebraska, Oklahoma, Iowa, Georgia, Kansas, Arizona, Nigeria, India, and Puerto Rico, likewise, are devoting a considerable portion of their resources to the development of an array of different types of breeding populations. It seems assured, therefore, that random-mating populations will pay a prominent role in sorghum breeding and development programs in future years.

MATERIALS AND METHODS

Development of IAP1R(M)C3

The half-sib and S_1 families evaluated in my experiments were derived from the third cycle of gridded mass selection in IAP1R(M) grain sorghum random-mating population. This population was developed by using lines that restored pollen fertility in the A_1 milo-kafir cytoplasmic-genetic male-sterility system. Development of the population was initiated in 1973 at Ames, Iowa by R. E. Atkins (Atkins, 1980), who made controlled crosses of ten restorer lines (including four converted exotic sorghums) onto bagged genetic male-sterile segregates from the NP3R sorghum random-mating population. Designations and pedigrees of the lines are given in Table 1. IAP1R possesses the $\underline{ms}_3$ gene for genetic male sterility, derived from the Coes variety via NP3R.

Seed from the 1973 crosses was composited so that the contribution of the ten restorer parents was equal. In 1974, a 600 g. sample of the composited seed was planted at Ames in an isolation plot of 0.09 ha (0.23 A), which contained approximately 6000 plants in 30 rows 30.5 m (100 ft.) long. Plants were spaced 15 cm apart in rows 102 cm apart, so that each plant could express its genetic potential fully. Thirty cells of a grid, each of equal size and rectangular shape (five rows 6.1 m [20 ft.] long), were superimposed on the isolated planting. All plants in this first generation (C0) were $\underline{Ms}_3\underline{ms}_3$ male fertile. Panicles borne on the main culms of fully male-fertile plants were tagged at anthesis. Tiller panicles were not tagged. Tagged panicles of combine

Table 1. Fertility restorer lines that were crossed onto bagged genetic male-sterile segregates of NP3R in 1973 to initiate IAP1R

Designation	Pedigree	Species or Sub-Group
IS2403c sel.	S_2 of BC_4 converted line from South Africa	Caudatum
IS3063c sel.	S_2 of temperate-zone bulk of converted line from Ethiopia	Caudatum
IS12567c sel.	S_2 of BC_4 converted line from Sudan	Durra-Nigricans
IS12608c sel.	S_2 of temperate-zone bulk of converted line from Ethiopia	Zera Zera
Redbine 58 x AK9-2 sel.	Redbine 58 = Martin x Combine 7008X-10 AK9-2 = Extra Early Pink x Early Kalo x Midland x Common Sudangrass	Kafir/Milo/Sudangrass
Redlan x OKY7 sel.	Redlan = CI1090 x CI71 OKY7 = Redlan x Short Kaura-1-10-1-1	Kafir/Kaura
Tx 7078	Kafir x Milo	Milo/Kafir
Tx 7000	Kafir x Milo	Milo/Kafir
Tx 2536	Caudatum/Kaura derivative	Caudatum/Kaura
NB 9040	(Korgi x CK60) x Texas Yellow	Kafir/Korgi

height (100-150 cm [40-60 in.]) were harvested from 15-25 plants per cell of the grid. The panicles chosen were from plants which appeared to possess at least average yielding ability; but no selection for panicle type, seed color, or seed size was practiced. Selected panicles were threshed individually and panicle yield and seed size (100-seed weight) were determined in the laboratory. Ten panicles that had the highest yields were chosen from each cell in the grid (300 panicles in all) to provide seed for the next generation.

Seed was composited from the 300 selected panicles (plants) and a 600 g. sample was planted in isolation at Ames in 1975. Male-sterile segregates appeared in this C1 generation. Tags of different colors were placed on the male-sterile and male-fertile plants so they could be differentiated at harvest. Tagged panicles were harvested from 15-25 phenotypically desirable male-fertile and male-sterile plants per cell of the grid. All harvested panicles were threshed individually, weighed, and a sample of 100 whole seeds was counted and weighed to determine seed size. Seed for the next generation was obtained by making a composite of seed from the 300 selected male-sterile panicles. The same procedures were followed each year through the C4 planting in 1978. Composites of seed from male-fertile and male-sterile plants harvested from the C4 were released to the public as IAP1R(M)C4 in 1979 (Mahlstede, 1979).

Experimental Procedure

Seed for my experiments came from the 1977 planting of the C3 generation of IAP1R(M). The theoretical value of the inbreeding

coefficient (F), was less than 0.5% for the C3. Seed from 600 tagged male-fertile plants and 450 tagged male-sterile plants had been placed in individual packets in cold storage in 1977. The intention was to evaluate the performance of 120 randomly chosen half-sib (derived from male-sterile panicles) and S_1 (derived from male-fertile panicles) families at Ames from 1978 through 1980 (Experiment I). Additionally, the plans were to evaluate another 120 S_1 families at Ames and in western Iowa (Castana) during 1981 and 1982 (Experiment II).

Experiment I was planted in Clarion-Webster soil at the Iowa State University Agronomy and Agricultural Engineering Research Center near Ames, Iowa. Planting dates were May 28, 22, and 22, respectively, in 1978, 1979, and 1980.

Experiment II was planted in Clarion-Webster soil at Ames and in Ida soil at the Western Iowa Research Center near Castana. Planting dates at Ames were May 19, 1981 and June 1, 1982. May 21, 1981 and June 2, 1982 were the dates of planting at Castana. A supplementary experiment, Experiment III, in which data were taken on individual plants in fourteen of the twenty highest yielding S_1 families from Experiment I, was planted at Ames in Clarion-Webster soil on June 1, 1982.

Each experimental site was fertilized in the spring with 112 kg/ha (100 lbs/A) of N just before planting. Applications of 90 kg/ha (80 lbs/A) of P_2O_5 and K_2O were made in each of the preceding fall seasons. Herbicidal weed control with Bexton (propachlor) applied at 13.05 liters/ha (5 quarts/A) was supplemented by mechanical cultivation and hand weeding. The insecticide Defend (Cygon) was applied at 1.63 liters/ha

(1.25 pints/A) each July at Ames, and Malathion at 1.96 liters/ha (1.5 pints/A) was applied similarly at Castana.

The experimental unit for Experiments I and II was a 3.05 m (10 ft.) section of a single row plot 4.27 m (14 ft.) long. Rows were spaced 102 cm (40 in.) apart. The experimental unit for Experiment III was a single plant within a row which was bordered by competitive plants. Data were taken on ten plants per row. Plants were thinned to stand 15 cm (6 in.) apart in rows 102 cm (40 in.) apart.

All experiments were planted by using a funnel planter. When seedlings reached the 3-4 leaf stage plots were thinned so that plants were approximately 8 cm (3 in.) apart in Experiment I, 10 cm (4 in.) in Experiment II, and 15 cm (6 in.) in Experiment III. The average plant populations established were 123,705 plants/ha (50,083 plants/A) in Experiment I, 97,200 plants/ha (39,352 plants/A) in Experiment II, and 65,360 plants/ha (26,461 plants/A) in Experiment III.

After thinning was completed in Experiments I and II, a 3.05 m (10 ft.) section of competitive plants was marked with a garden stake at each end. When there were not 3.05 m of competitive plants in a row, a shorter plot (but not less than 1.53 m [5 ft.]) was marked. Plants within the staked sections were counted and the number of plants/plot was recorded. Determinations of grain yield/unit area, plants/plot, and panicles/plot in short plots were adjusted arithmetically to the standard 3.05 m length.

Data were recorded in 1982 at Ames for height and days to midbloom for the S_1 lines in Experiment II and for the individual plants in the

S_1 families of Experiment III. Plant height was measured during the grain filling period, as the distance from the soil surface to the tip of the panicle on the main culm. Days to midbloom was defined as the number of days from planting until anthesis was completed halfway down the panicle of the main culm.

Plots were harvested in October each year after a killing frost, when grain moisture ranged from 25-30%. Panicles from the staked sections in each plot were counted as they were severed from the plants by cutting the peduncle just below the lowest panicle branch. For Experiments I and II, two representative panicles were harvested from each plot and rubber-banded together so they could be retrieved for threshing and determination of seed size. All panicles harvested from each plot were placed in an Osnaburg (AM size) cloth bag and dried artificially for three days at 71.1°C (160°F). Grain in the panicles attained a moisture content of about 5 to 7%, and plot weights were then recorded in hundredths of a pound.

A regression equation was developed for Experiments I and II in each year which converted dry weight of panicles/plot to grain yield in quintals per hectare (Robinson and Bernat, 1963). Six plots that were above the experiment mean in dry panicle weight, and six that were below the mean, were chosen randomly. Panicles from these plots were threshed by using an Almaco LPT All Purpose Plot Thresher and grain weights were determined. A regression equation was then fitted by using the threshed grain weights (Y) and dry panicle weights (X) in pounds.

Let $\bar{X}_a$ = mean of six plots with dry panicle weights above the mean of all plots.

$\bar{X}_b$ = mean of six plots with dry panicle weights below the mean of all plots.

$\bar{Y}_a$ = mean threshed grain weight of the six plots above the mean of all plots for dry panicle weight x 14.64 (a factor to express grain yield on a q/ha basis).

$\bar{Y}_b$ = mean threshed grain weight of the six plots below the mean of all plots for dry panicle weight x 14.64.

$\bar{X}$ = mean dry panicle weight for the twelve selected plots.

$\bar{Y}$ = mean threshed grain weight (q/ha) for the twelve selected plots.

$b = (\bar{Y}_a - \bar{Y}_b)/(\bar{X}_a - \bar{X}_b)$

$a = \bar{Y} - b\bar{X}$

$Y = a + bX$ is the form of the completed regression equation.

The equations developed to convert lbs/plot of dry panicles to q/ha of threshed grain were:

Experiment I	Ames 1978	$Y = -4.65 + 12.59X$,
	Ames 1979	$Y = -4.19 + 12.69X$,
	Ames 1980	$Y = -8.52 + 13.12X$,
Experiment II	Ames 1981	$Y = 0.473 + 11.76X$,
	Castana 1981	$Y = -7.72 + 13.15X$,
	Ames 1982	$Y = 2.60 + 10.49X$, and
	Castana 1982	$Y = -3.07 + 11.87X$.

The regression procedure for determining grain yield was not used

in Experiment III. Instead, the panicles harvested from each of the individual plants were threshed collectively by using a Vogel Plant Thresher and the composite of seed was weighed and recorded in g/plant.

Seed size was determined in Experiments I and II from the grain obtained from each two-panicle plot sample. For Experiment III, a sample of the threshed grain from each harvested plant was used. One hundred whole kernels were counted from each bulk sample and then weighed to the nearest centigram by using an electronic balance.

Individual plants in Experiment III were also rated for panicle type and pollen fertility. For panicle type a scale of 1 to 3 was used; 1 = compact, 2 = semi-compact, 3 = open. Plants were rated as either male-fertile or male-sterile by visual observation of the presence or absence of pollen.

Data for several other characters were calculated by using the values for the directly-observed variables; i.e., plants/plot, panicles/plot, seed size, and grain yield/plot. The additional characters were:

Panicles/plant = panicles/plot ÷ plants/plot,

Yield/plant = plot grain yield (g) ÷ plants/plot,

Yield/panicle = plot grain yield (g) ÷ panicles/plot,

$$\text{Seeds/panicle} = \frac{\text{plot grain yield (g)}}{\text{panicles/plot} \times 100 \text{ seed weight (g)}} \times 100, \text{ and}$$

Seeds/plant = seeds/panicle x panicles/plant.

Statistical Procedure

A sets within replicates design was used for Experiments I and II. In Experiment I there were two replicates each year, with six sets

containing both family types (half-sib and S_1) in each replicate. In Experiment II, there were two replicates at each location in each year, with six sets of S_1 lines in each replicate. Twenty genotypes per set were planted in both experiments, but incomplete data for some genotypes caused some sets to have data from less than twenty genotypes for some variables. All effects except those attributable to sets were considered random. The primary objective of the experiments was to estimate the variance components σ^2 (error variance), σ^2_{ge} (genotype-environment interaction variance), and σ^2_g (genetic variance). A completely random model was assumed for estimation of the variance components in the combined analysis of each experiment.

The linear model for each year's analysis in Experiment I was:

$$Y_{ijkq} = \mu + R_i + S_{j(i)} + F_q + L_{k(jq)} + e_{iq(jk)}$$

where i = 1 ... r replications, j = 1 ... s sets, k = 1 ... ℓ genotypes for each family type, q = 1 ... f family types, and Y_{ijkq} = observed value for the kth genotype of the qth family type within the jth set and the ith replicate; μ = overall mean; R_i = effect of the ith replicate; $S_{j(i)}$ = effect of the jth set within the ith replicate; F_q = effect of the qth family type; $L_{k(jq)}$ = effect of the kth genotype within the qth family type and jth set; $e_{iq(jk)}$ = experimental error.

The combined analysis for Experiment I was carried out by using the genotype means for each year. Sums of squares from this analysis were multiplied by r (2) to put them on a per plot bais. The error term was obtained by pooling the error terms from each year's ANOVA. Data were analyzed assuming the following linear model:

Table 2. Form of the ANOVA for Experiment I for each year

Source of variation	df	Mean square	Expected mean squares	F test
Replications (Rep)	r-1			
Sets/Rep	r(s-1)			
Genotypes/Sets	s(fℓ-1)	M3	$\sigma^2 + r\sigma^2_f$	M3/M7
S_1/Sets	s(ℓ-1)	M4	$\sigma^2_1 + r\sigma^2_{S1}$	M4/M8
HS/Sets	s(ℓ-1)	M5	$\sigma^2_2 + r\sigma^2_{HS}$	M5/M9
S_1 vs HS/Sets	s(f-1)	M6		M6/M7
Error	s(fℓ-1)(r-1)	M7	σ^2	
S_1	s(ℓ-1)(r-1)	M8	σ^2_1	
HS	s(ℓ-1)(r-1)	M9	σ^2_2	

$$Y_{hjkq} = \mu + M_h + S_j + MS_{hj} + F_q + L_{k(jq)} + ML_{hk(jq)}$$

where h = 1 ... m environments or years; j = 1 ... s sets; k = 1 ... ℓ genotypes; q = 1 ... f family types; and Y_{hjkq} = observed value for the kth genotype with the qth family type within the jth set and the hth environment; μ = overall mean; M_h = effect of the hth environment; S_j = effect of the jth set; MS_{hj} = the effect of the interaction of the jth set with the hth environment; F_q = effect of the qth family type; $L_{k(jq)}$ = effect of the kth genotype within the qth family type and the jth set; $ML_{hk(jq)}$ = effect of the interaction of the hth environment with the kth genotype nested within the jth set and qth family type.

Table 3. Form of the ANOVA for the combined analysis of Experiment I

Source of variation	df	Mean square	Expected mean squares	F test
Environments (Envir.)	m-1			
Sets	s-1			
Envir. x Sets	(m-1)(s-1)			
Genotypes/Sets	s(fℓ-1)	M4	$\sigma^2 + r\sigma^2_{ge} + rm\sigma^2_g$	M4/M8
S_1/Sets	s(ℓ-1)	M5	$\sigma^2_1 + r\sigma^2_{S1\cdot m} + rm\sigma^2_{S1}$	M5/M9
HS/Sets	s(ℓ-1)	M6	$\sigma^2_2 + r\sigma^2_{HS\cdot m} + rm\sigma^2_{HS}$	M6/M10
S_1 vs HS/Sets	s(f-1)	M7		M7/M8
Envir. x Genotypes/ Sets	s(fℓ-1)(m-1)	M8	$\sigma^2 + r\sigma^2_{ge}$	M8/M12
S_1/Sets	s(ℓ-1)(m-1)	M9	$\sigma^2_1 + r\sigma^2_{S1\cdot m}$	M9/M13
HS/Sets	s(ℓ-1)(m-1)	M10	$\sigma^2_2 + r\sigma^2_{HS\cdot m}$	M10/M14
S_1 vs HS/Sets	s(f-1)(m-1)	M11		M11/M12
Pooled error	ms(fℓ-1)(r-1)	M12	σ^2	
S_1	ms(ℓ-1)(r-1)	M13	σ^2_1	
HS	ms(ℓ-1)(r-1)	M14	σ^2_2	

S_1 families only were tested in Experiment II. The model for each location/year analysis was:

$$Y_{ijk} = \mu + R_i + S_{j(i)} + L_{k(j)} + e_{ijk}$$

in which all effects are the same as described for Experiment I except $L_{k(j)}$. $L_{k(j)}$ = effect of the kth genotype within the jth set. The form of the location/year ANOVAs was the same as shown for Experiment I, except that there was no breakdown into family types.

The model for the combined analysis of Experiment II was:

$$Y_{ijkh} = \mu + R_{i(h)} + S_{j(i)} + M_h + SM_{j(i)h} + L_{k(j)} + LM_{k(j)h} + e_{i(jk)h}$$

where i = 1 ... r replications; j = 1 ... s sets; k = 1 ... ℓ genotypes; h = 1 ... m environments; Y_{ijkh} = observed value for the kth genotype within the jth set and ith replicate in the hth environment; μ = overall mean; $R_{i(h)}$ = effect of the ith replicate within the hth environment; $S_{j(i)}$ = effect of the jth set within the ith replicate; M_h = effect of the hth environment; $SM_{j(i)h}$ = effect of the interaction of the jth set within the ith replicate with the hth environment; $L_{k(j)}$ = effect of the kth genotype within the jth set; $LM_{k(j)h}$ = effect of the interaction of the kth genotype within the jth set with the hth environment, $e_{i(jk)h}$ = experimental error.

Table 4. Form of the ANOVA for the combined analysis of Experiment II

Source of variation	df	Mean squares	Expected mean squares	F test
Environments (Envir.)	m-1			
Replications/Envir.	m(r-1)			
Sets/Reps	r(s-1)			
Envir. x Sets/Reps.	(m-1)(s-1)r			
Genotypes/Sets	s(ℓ-1)	M5	$\sigma^2 + r\sigma^2_{ge} + rm\sigma^2_g$	M5/M6
Envir. x Genotypes/ Sets	(m-1)(ℓ-1)s	M6	$\sigma^2 + r\sigma^2_{ge}$	M6/M7
Error	(r-1)(m-1)(ℓ-1)s	M7	σ^2	

An analysis of variance was not performed on the data of Experiment III. There was insufficient remnant seed of the S_1 families tested to allow replication. Therefore, only means will be presented.

Data Analysis

The field data collected during the 1978 through 1982 seasons were transferred to punched cards and analyzed using the facilities of the Iowa State University Computation Center, Ames, Iowa. These data were analyzed using SAS (Statistical Analysis System, the SAS Institute Inc., Cary, North Carolina). In addition, parts of the combined analysis of Experiment II were analyzed using LSML76 (Mixed Model Least Squares and Maximum Likelihood Computer Program), developed by Walter R. Harvey, Ohio State University (1977). The LSML76 program allowed the estimation of variance components with unbalanced data sets in a mixed model using Method 3 of Henderson (1953).

Estimation of Variance Components

Variance components for each trait were estimated from expected mean squares for the sources of variation of interest. These sources were genotypes, genotypes x environments, and error in the combined analysis of variance for Experiments I and II. In Experiment I, the numerical values of the coefficients in the expected mean squares were $r = 2$, $m = 3$, and $rm = 6$. In Experiment II, because of missing values, $r = 1.9040$ instead of 2, $m = 3.9178$ instead of 4, and $rm = 7.4602$ instead of 8.

Standard errors of variance components were computed using the formula:

$$\left[\frac{2}{C^2}\left(\sum_i M.S._i^2/(df_i + 2)\right)\right]^{1/2}$$

where C = coefficient of the component in the expected mean squares; $M.S._i$ = mean square for the ith trait; df_i = degrees of freedom for the ith trait.

Heritabilities were calculated as the ratio of genetic variance (σ_g^2) to phenotypic variance (σ_{ph}^2). Heritabilities and their standard errors were estimated for the S_1 and half-sib families by using the following formulae:

Entry mean basis

$$\frac{\hat{\sigma}_g^2}{\frac{\hat{\sigma}^2}{rm} + \frac{\hat{\sigma}_{ge}^2}{m} + \hat{\sigma}_g^2} \qquad S.E. = \frac{S.E.\ \hat{\sigma}_g^2}{\frac{\hat{\sigma}^2}{rm} + \frac{\hat{\sigma}_{ge}^2}{m} + \hat{\sigma}_g^2}$$

Plot basis

$$\frac{\hat{\sigma}_g^2}{\hat{\sigma}^2 + \hat{\sigma}_{ge}^2 + \hat{\sigma}_g^2} \qquad S.E. = \frac{S.E.\ \hat{\sigma}_g^2}{\hat{\sigma}^2 + \hat{\sigma}_{ge}^2 + \hat{\sigma}_g^2}$$

Individual-plant-basis heritabilities were estimated using the method of parent-offspring regression involving male-fertile plants and their S_1 families. The regression coefficient $b = \frac{\sigma_{xy}}{\sigma_x^2}$ when x = (individual S_0 plant measurement for a trait minus the mean of all harvested plants

from that cell of the grid); y = (S_1 family mean over all environments for a trait minus the mean of all members of the same set). The value calculated for b gives a broad sense, individual-plant, heritability $\frac{\sigma_A^2 + 1/2\sigma_D^2 + \sigma_{AA}^2 + ..}{\sigma_{ph}^2}$. The standard error of the individual-plant heritability was calculated as S.E. b.

Phenotypic correlations among traits were calculated using options of SAS and LSML76. Genetic correlations were calculated using mean products and estimates of genetic variances obtained from the combined analyses of variance. The general formula used was:

$$r_g = \frac{\sigma_{gxy}}{\sqrt{\hat{\sigma}^2_{g_x} \cdot \hat{\sigma}^2_{g_y}}}$$

where σ_{gxy} = the genetic covariance between traits x and y; $\hat{\sigma}^2_{g_x}$ = estimate of genetic variance for trait x; $\hat{\sigma}^2_{g_y}$ = estimate of genetic variance for trait y.

Expected responses to selection obtained by recombining selected families or individuals were calculated using data from the combined analyses. The basic formula, which may be modified to account for different numbers of generations per year and per cycle, was $\Delta G = k\sigma_{ph}h^2$ where ΔG = expected gain from selection; k = standardized selection differential; σ_{ph} = square root of the phenotypic variance; h^2 = heritability. For individual plant selection k = 1.40 (20% selection intensity), σ_{ph} = square root of the phenotypic variances among plants

in the isolation planting, and h^2 = the estimate of b obtained from the parent-offspring regression. For family selection, k = 1.40, σ_{ph} = square root of the phenotypic variance among families of a given type, and h^2 = family genetic variance divided by family phenotypic variance.

Correlated responses to selection were calculated using the formula $CRy(x) = k_x \cdot \sqrt{h_x^2} \cdot r_{g_{x,y}} \cdot \sigma_{g_y}$ where CRy(x) = expected correlated response in trait y when selection is for trait x; k_x = standardized selection differential applied in selection for trait x; $\sqrt{h_x^2}$ = square root of the heritability of trait x; $r_{g_{x,y}}$ = genetic correlation between traits x and y; σ_{g_y} = square root of the estimate of genetic variance for trait y.

Estimates of additive genetic variance for the various traits measured in IAP1R(M)C3 were obtained by using estimates from half-sib families. Because the genetic variance among half-sib families is expected to be one-fourth of the additive genetic variance, total additive genetic variance in the population was estimated by multiplying the estimates of genetic variance among half-sib families by four. The genetic coefficient of variation, a measure of genetic variability in a population in relation to the mean for a particular trait, was calculated as $\frac{\sqrt{\hat{\sigma}_A^2}}{\overline{X}} \times 100$ where $\hat{\sigma}_A^2$ = estimate of additive genetic variance and $\overline{X}$ = mean value for a given trait.

An estimate of inbreeding depression for the different traits was obtained from Experiment I. Half-sib families were derived from male-sterile plants that were pollinated at random. Therefore, half-sib families may be considered non-inbred (F = 0). S_1 families, in contrast, were derived from male-fertile plants that were mainly self-pollinated. Thus S_1 families are inbred one generation (F = 1/2), and since homozygosity increases by 50% each generation under a system of self-pollination, the mean of S_1 families for a given trait should reflect one-half of the total inbreeding depression that would occur. An estimate of total inbreeding depression was, therefore, calculated for traits for which there was a significant difference between half-sib and S_1 means. The formula was $\frac{\overline{X}_{HS} - \overline{X}_{S_1}}{\overline{X}_{HS}} \times 200$, where $\overline{X}$ = family mean and HS and S_1 refer to half-sib and S_1 families, respectively.

RESULTS

Environmental conditions during the 1977 growing season at Ames affected my experiments indirectly, because all the seed for my experiments came from plants grown in the 1977 isolation planting of IAP1R(M). Dry conditions that year delayed planting until June 15 (25 days later than normal) and seedlings did not emerge until June 30. There was a paucity of rainfall in June and July, but that August was the wettest on record, 305 mm (12 in.), and cool. Consequently, anthesis occurred later than usual and grain-filling proceeded slowly as cool temperatures continued in September. Seed harvested that year (Appendix, Table A1) was abnormally small, and seed of later-maturity genotypes did not ripen fully before the first frost.

Experiment I

Although all plots were overseeded by planting approximately 59-66 seeds/m (18-20 seeds/ft.) to achieve final stands of 13 plants/m (4 plants/ft.), seedling emergence was so poor for some entries that full sections of 3.05 m of competitive plants were not obtained. Consequently, there were many short plots of less than 3.05 m, and there were several entries which had such poor emergence that sections of competitive plants were smaller than the minimum requirement of 1.5 m. As a result, the number of families analyzed for Experiment I was not the planned 120 half-sib and S_1 families, but 102 half-sib and 101 S_1 families.

Environmental conditions at Ames were excellent for sorghum production in 1978 and 1979, and good in 1980. Individual year means

for the nine traits measured are presented in the Appendix (Table A2). Average grain yields of all entries ranged from a low of 62.8 q/ha in 1980 to a high of 67.8 q/ha in 1979, and seed size was 14-21% greater than in the 1977 isolation planting.

In the combined ANOVA (for each year's ANOVA see Appendix, Tables A3-A5) for Experiment I (Table 5), it should be noted that there were one S_1 family and one half-sib family with missing values for several traits in 1980, and that one degree of freedom was substracted from error degrees of freedom for those traits. Differences among all entries (genotypes/sets) were highly significant ($p \leq 0.01$) for all traits. Among S_1 families, there were significant ($p \leq 0.05$) differences for the trait plants/plot and highly significant differences for all other traits. Among half-sib families, there were highly significant differences for all traits. There were no significant differences between half-sib and S_1 families for the traits panicles/plant, plants/plot, and panicles/plot. There were highly significant differences for all other traits.

The genotype-environment interaction for all entries (environment x genotypes/sets) was non-significant for 100-seed weight and plants/plot, significant for grain yield, and highly significant for all other traits. The genotype-environment interaction for S_1 families was not significant for grain yield, 100-seed weight, and plants/plot, significant for grain yield/plant, and highly significant for all other traits. The half-sib family genotype-environment interaction was non-significant for all traits except panicles/plant and grain yield/panicle, which were

Table 5. Mean squares from the combined ANOVA for traits measured in Experiment I, Ames, 1978 through 1980

Source of variation	df	Mean squares: Grain yield	Seeds/ panicle	100-seed weight
			(x 100)	(x 10)
Environments (Envir.)	2	2582.7	1411.1	338.1
Sets	5	311.9	87.6	120.1
Sets x Envir.	10	175.5	9.4	13.2
Genotypes/Sets	197	306.8**	23.0**	43.3**
S_1/Sets[a]	95	329.8**	27.5**	53.6**
HS/Sets[a]	96	227.0**	18.1**	32.2**
S_1 vs HS/Sets	6	1221.2**	29.3**	58.8**
Envir. x Genotypes/Sets	394	44.6*	5.1**	8.9^{ns}
Envir. x S_1/Sets	190	48.0^{ns}	5.9**	9.7^{ns}
Envir. x HS/Sets	192	36.7^{ns}	4.4^{ns}	8.3^{ns}
Envir. x S_1 vs HS/Sets	12	117.1**	5.7^{ns}	5.5^{ns}
All entries pooled error	591[b]	37.7	4.0	9.2
S_1 entries pooled error	285[b]	44.2	3.7	8.4
HS entries pooled error	288[b]	31.8	4.3	10.0
All entries C.V. (%)		10.2	15.9	10.5
S_1 entries C.V. (%)		11.0	17.2	11.1
HS entries C.V. (%)		8.9	14.5	10.1

[a]HS = half-sib family; S_1 = S_1 family; as used in this and all subsequent tables.

[b]Because of missing values, the traits seeds/panicle, panicles/plant, grain yield/panicle, and panicles/plot had 1 degree of freedom less than indicated for S_1 and HS errors, and 2 degrees of freedom less for overall error.

*,**Indicate significance beyond the 0.05 and 0.01 probability levels, respectively; ns = not significant; as used in this and all subsequent tables.

Mean squares					
Panicles/ plant	Grain yield/ panicle	Grain yield/ plant	Plants/ plot	Panicles/ plot	Seeds/ plant
(x 10)					(x 100)
440.6	9409.5	3436.1	239.8	7922.5	1048.3
18.2	528.2	436.4	23.6	310.2	135.4
17.2	67.3	286.5	35.0	86.2	71.7
9.8**	137.0**	281.6**	16.3**	101.4**	43.6**
10.7**	144.7**	282.1**	17.4*	114.4**	49.8**
9.2**	112.0**	234.9**	15.7**	91.4**	36.0**
5.2^{ns}	416.2**	1018.8**	9.8^{ns}	56.4^{ns}	66.6**
3.9**	22.4**	57.1**	11.3^{ns}	35.5**	13.0**
3.6**	25.4**	52.7*	12.4^{ns}	36.1**	12.5**
3.4*	18.2*	52.6^{ns}	9.6^{ns}	30.7^{ns}	11.4^{ns}
14.6**	42.9**	199.1**	22.0*	102.6**	45.0**
2.6	14.9	44.0	10.6	27.0	9.6
2.2	15.4	39.4	10.4	23.6	8.5
2.5	14.0	44.8	10.5	27.5	10.4
14.3	11.9	14.2	8.8	11.5	18.7
14.1	13.1	14.2	9.1	11.6	18.8
13.4	10.4	13.1	8.1	10.6	17.1

significant. The S_1 vs HS comparison showed a non-significant interaction with environment for the traits seeds/panicle and 100-seed weight, a significant interaction for plants/plot, and a highly significant interaction for all other traits.

Coefficients of variation for all entries ranged from 8.8% for plants/plot to 18.7% for seeds/plant. It is encouraging to note that grain yield had the second lowest coefficient of variation. Half-sib families had lower coefficients of variation than S_1 families for all traits.

Population means and ranges for grain yield, yield components, and other agronomic traits (Table 6) are important for assessing the potential value of a population as a source of inbred lines. This is true because continuous selfing without recombination merely fixes genotypes, and the genotype of the S_0 plant chosen sets the upper limit. Of course, high yielding inbred lines with good agronomic traits have to be tested empirically to assess their comining ability in hybrid combinations. The mean yield of all entries over all environments was 65.6 q/ha, and individual genotype yields ranged from 40.6-86.2 q/ha. For comparison, mean yield of the commercial hybrids RS610 and RS671 grown in adjacent plots in the same environments was 94 q/ha. Thus the population mean yield (based on the half-sib mean of 67.9 q/ha) was 72% of the hybrid mean in these favorable environments, and certain genotypes yielded up to 92% of the hybrids. Means and ranges for the primary yield components (seeds/panicle, 100-seed weight, and panicles/plant) show that there is great variability among lines from the population.

Table 6. Means, maximum and minimum genotype values, and genotype L.S.D.$_{.05}$ for traits measured in the combined ANOVA for Experiment I, Ames, 1978 through 1980

Trait	Genotype values		
	Mean		
	All entries	HS	S_1
Grain yield (q/ha)	65.6 ± 0.2	67.9 ± 0.2	63.3 ± 0.3
Seeds/panicle	1428 ± 6	1451 ± 8	1405 ± 10
100-seed weight (g)	2.83 ± 0.01	2.87 ± 0.01	2.80 ± 0.01
Panicles/plant	1.37 ± 0.01	1.38 ± 0.01	1.35 ± 0.01
Grain yield/panicle (g)	39.7 ± 0.1	40.9 ± 0.2	38.4 ± 0.2
Grain yield/plant (g)	53.3 ± 0.2	55.4 ± 0.3	51.2 ± 0.3
Plants/plot	38.3 ± 0.1	38.2 ± 0.1	38.5 ± 0.1
Panicles/plot	51.9 ± 0.2	52.1 ± 0.1	51.7 ± 0.2
Seeds/plant	1926 ± 10	1976 ± 14	1876 ± 14

[a]Difference in genotype means needed for significance at 0.05 probability level.

Genotype values								
Minimum			Maximum			Genotype L.S.D.$_{.05}$[a]		
All entries	HS	S_1	All entries	HS	S_1	All entries	HS	S_1
40.6	40.6	46.4	86.2	86.2	81.4	7.6	6.8	7.8
888	940	888	1973	1973	1947	257	237	274
1.94	1.94	2.06	3.57	3.47	3.57	0.34	0.33	0.35
1.06	1.08	1.06	1.86	1.75	1.86	0.22	0.21	0.22
26.4	26.4	28.0	53.2	53.2	49.3	5.4	4.8	5.7
31.8	31.8	37.7	73.7	72.7	73.7	8.6	8.2	8.2
34.0	34.0	34.2	43.0	41.5	43.0	3.8	3.5	4.0
40.5	40.5	42.8	67.0	67.0	65.7	6.7	6.3	6.8
1181	1416	1181	2811	2626	2811	408	383	400

Quantitatively inherited traits such as grain yield may show a change in the population mean upon inbreeding. Loci at which there is a degree of dominance, such that the heterozygote has a value greater than the average of the homozygotes, will show inbreeding depression. The contribution of each locus will depend on gene frequencies, those with intermediate values (ca. 0.5) having the most effect. There were highly significant differences between the population means for half-sib (F = 0) and S_1 (F = 1/2) families (Table 7) for all traits except panicles/plant, panicles/plot, and plants/plot. The estimate of total inbreeding depression at S_∞ (F = 1) assumes that the mean decreases in a linear manner as F increases. Seed size seems to be controlled largely by additive gene action because inbreeding depression at 100% homozygosity was estimated to be less than 5%. Characters that involve numbers of seeds, such as seeds/panicle and seeds/plant, showed slightly greater inbreeding depression and thereby more non-additive gene action. The greatest amount of inbreeding depression (12-15%) was observed for the different measures of grain yield. The low estimates of inbreeding depression for grain yield are not surprising because grain sorghums are predominantly self-pollinating.

Estimates of variance components for the two family types (Table 8) were obtained from the mean squares in the combined ANOVA for pooled error (σ^2), genotypes/sets x environments (σ^2_{ge}), and genotypes/sets (σ^2_g). Estimates of error variances were lower for S_1 families than for half-sib families for all traits except the grain yield traits. Estimates of error variances were similar in magnitude to estimates of genetic

Table 7. Trait means and estimates of total inbreeding depression (from S_0 to S_∞) for traits measured in Experiment I, Ames, 1978 through 1980

Trait	Mean		F test	Estimate of total inbreeding depression
	HS	S_1	S_1 vs HS	
				(%)
Grain yield (q/ha)	67.9	63.3	**	-13.6
Seeds/panicle	1451	1405	**	-6.3
100-seed weight (g)	2.87	2.80	**	-4.9
Panicles/plant	1.38	1.35	n.s.	--
Grain yield/panicle (g)	40.9	38.4	**	-12.2
Grain yield/plant (g)	55.4	51.2	**	-15.2
Plants/plot	38.2	38.5	n.s.	--
Panicles/plot	52.1	51.7	n.s.	--
Seeds/plant	1976	1876	**	-10.1

Table 8. Estimates of variance components for traits measured in Experiment I, Ames, 1978 through 1980

Trait	Variance component			
	σ^2	σ^2_{ge}	σ^2_g	σ^2_{ph}
Grain yield (q/ha)				
S_1	44.18 ± 3.69	1.92 ± 3.07	46.97 ± 7.94	54.98 ± 7.89
HS	31.81 ± 2.64	2.45 ± 2.28	31.71 ± 5.44	37.82 ± 5.40
Seeds/panicle (x 100)				
S_1	3.7 ± 0.3	1.1 ± 0.3	3.6 ± 0.7	4.6 ± 0.7
HS	4.3 ± 0.4	0.04 ± 0.3	2.3 ± 0.4	3.0 ± 0.4
100-seed weight (x 10) (g)				
S_1	8.4 ± 0.7	0.7 ± 0.6	7.3 ± 1.3	8.9 ± 1.3
HS	10.0 ± 0.8	-0.8 ± 0.6	4.0 ± 0.8	5.4 ± 0.8
Panicles/plant (x 10)				
S_1	2.2 ± 0.2	0.7 ± 0.2	1.2 ± 0.3	1.8 ± 0.3
HS	2.5 ± 0.2	0.4 ± 0.2	1.0 ± 0.2	1.5 ± 0.2
Grain yield/panicle (g)				
S_1	15.40 ± 1.29	5.02 ± 1.45	19.88 ± 3.49	24.11 ± 3.46
HS	14.02 ± 1.17	2.10 ± 1.09	15.63 ± 2.68	18.67 ± 2.67
Grain yield/plant (g)				
S_1	39.44 ± 3.29	6.61 ± 3.15	38.25 ± 6.81	47.02 ± 6.75
HS	44.85 ± 3.72	3.90 ± 3.26	30.38 ± 5.66	39.15 ± 5.59
Plants/plot				
S_1	10.38 ± 0.87	0.99 ± 0.77	0.84 ± 0.47	2.90 ± 0.42
HS	10.53 ± 0.87	-0.46 ± 0.65	1.01 ± 0.41	2.61 ± 0.37
Panicles/plot				
S_1	23.56 ± 1.97	6.26 ± 2.08	13.06 ± 2.81	19.08 ± 2.74
HS	27.54 ± 2.29	1.58 ± 1.93	10.11 ± 2.24	15.23 ± 2.18
Seeds/plant (x 100)				
S_1	8.5 ± 0.7	2.0 ± 0.7	6.2 ± 1.2	8.3 ± 1.2
HS	10.4 ± 0.9	0.5 ± 0.7	4.1 ± 0.9	6.0 ± 0.9

variance for all traits except plants/plot, and to a lesser extent for the traits panicles/plant and panicles/plot. Estimates of genotype-environment interaction variance were small relative to estimates of error variance for all traits, and relative to genetic variance for all traits except plants/plot. S_1 families had greater genotype-environment interaction variances than half-sib families for all traits except grain yield/unit area. There were larger estimates of genetic variance for S_1 families than for half-sib families for all traits except plants/plot. The reason that variance estimates for plants/plot were somewhat anomalous may be that the seeding rate was so high that genetic differences in germination percentage and stand estabishment were obscured. Phenotypic variance estimates always were larger for S_1 families than for the half-sib families.

Estimates of additive genetic variance (Table 9) were obtained for the traits measured based on the genetic expectation that the variance among half-sib families is one-fourth of the additive genetic variance. The major assumptions required for this premise are (1) the population is random mating and there is adequate sampling of randomly chosen genotypes, (2) linkage equilibrium in the reference population, (3) no maternal effects, (4) no multiple alleles, (5) normal diploid behavior, (6) no environmental correlation with genotypes, and (7) no epistasis. Estimates of S_1 family variance are presented in the same table for comparison. In every instance, $\hat{\sigma}^2_A$ is larger than $\hat{\sigma}^2_{S_1}$, and the ratio $\hat{\sigma}^2_A/\hat{\sigma}^2_{S_1}$ ranged from 2.2 for 100-seed weight to 4.8 for plants/plot. The ratio for grain

yield was 2.7. The implication is that $\hat{\sigma}^2_A$ was overestimated and/or $\hat{\sigma}^2_{S_1}$ was underestimated.

Table 9. Estimates of additive genetic variance, genetic coefficients of variation, and S_1 family variance for traits measured in Experiment I, Ames, 1978 through 1980

Trait	$\hat{\sigma}^2_A$	Genetic coefficient of variation	$\hat{\sigma}^2_{S_1}$
		(%)	
Grain yield (q/ha)	126.84 ± 21.76	16.6	46.97 ± 7.94
Seeds/panicle (x 100)	9.2 ± 1.6	20.8	3.6 ± 0.7
100-seed weight (x 10) (g)	16.0 ± 3.2	14.0	7.3 ± 1.3
Panicles/plant (x 10)	4.0 ± 0.8	14.2	1.2 ± 0.3
Grain yield/panicle (g)	62.52 ± 10.72	19.3	19.88 ± 3.49
Grain yield/plant (g)	121.52 ± 22.64	19.9	38.25 ± 6.81
Plants/plot	4.04 ± 1.64	5.3	0.84 ± 0.47
Panicles/plot	40.44 ± 8.96	12.2	13.06 ± 2.81
Seeds/plant (x 100)	16.4 ± 3.6	20.5	6.2 ± 1.2

A measure of the genetic variation in the population relative to the mean is the genetic coefficient of variation (Table 9). As expected, the trait plants/plot (5.3%) showed the least variation. There was great variability in the population for seeds/panicle (20.8%) and seeds/plant (20.5%). The genetic coefficient of variation for the grain yield traits ranged from 16.6-19.9%. There was less variation for panicles/plant (14.2%), the capacity of the plant to produce panicle-bearing basal or axillary tillers. Seed size had a genetic coefficient of variability of 14%. These estimates and the estimates of means presented earlier

(Table 6) indicate that three generations of gridded mass selection in isolation plantings with adequate (300 plants) sampling (10% selection intensity) has been effective in achieving recombination and some breakage of linkage blocks, without adverse effects on the population means.

Knowledge of heritabilities (Table 10) for grain yield, primary yield components, and other agronomic traits is of considerable importance in plant breeding, because it facilitates a rational choice of selection methods based on predictions of expected gains from selection. In this table, the family genetic variance, $\sigma^2_{g_{HS}} = 1/4\sigma^2_A$ for half-sib families and $\sigma^2_{g_{S_1}} = \sigma^2_{A*} + 1/4\sigma^2_D$ for S_1 families, was divided by the appropriate phenotypic variance term to obtain estimates of progeny mean and plot basis heritabilities. The estimate of additive genetic variance ($\hat{\sigma}^2_A$) was not used in calculating any of these heritabilities. On a progeny mean basis, estimates of heritability were slightly higher for S_1 families than for half-sib families for all traits except plants/plot and grain yield/panicle, although in no case was the difference greater than the standard error of the estimate. The grain yield traits were the most heritable, and plants/plot was the least heritable. Heritabilities for grain yield (0.84 and 0.85 for half-sib and S_1 families, respectively) were high because the near optimum environments allowed genotypes to express their full genetic potential, and because genotype-environment interactions were low. S_1 and half-sib heritabilities on a plot basis were highest for grain yield/unit area (HS = 0.48,

Table 10. Estimates of heritability for traits measured in Experiment I, Ames, 1978 through 1980

Trait	Heritability				
	Progeny mean basis		Plot basis		Individual plant basis
	HS	S_1	HS	S_1	$S_1 - S_0$
Grain yield/unit area	0.84 ± 0.14	0.85 ± 0.14	0.48 ± 0.08	0.50 ± 0.09	0.13 ± 0.07
Seeds/panicle	0.76 ± 0.15	0.79 ± 0.15	0.34 ± 0.07	0.43 ± 0.08	0.20 ± 0.04
100-seed weight	0.74 ± 0.15	0.82 ± 0.14	0.30 ± 0.06	0.45 ± 0.08	0.41 ± 0.06
Panicles/plant	0.63 ± 0.15	0.66 ± 0.15	0.24 ± 0.06	0.29 ± 0.06	---
Grain yield/panicle	0.84 ± 0.14	0.82 ± 0.14	0.49 ± 0.08	0.49 ± 0.09	---
Grain yield/plant	0.78 ± 0.14	0.81 ± 0.14	0.38 ± 0.07	0.45 ± 0.08	---
Plants/plot	0.39 ± 0.16	0.29 ± 0.16	0.09 ± 0.04	0.07 ± 0.04	---
Panicles/plot	0.66 ± 0.15	0.68 ± 0.15	0.26 ± 0.06	0.30 ± 0.07	---
Seeds/plant	0.68 ± 0.15	0.75 ± 0.15	0.27 ± 0.06	0.37 ± 0.07	---

S_1 = 0.50) and for the other measures of grain yield (grain yield/plant and grain yield/panicle). Estimates for S_1 families were greater or equaled those for half-sib families for all traits except plants/plot. Estimates of individual plant heritabilities were lower than those calculated on a plot mean basis except for 100-seed weight, which was more heritable on an individual plant basis than on a half-sib family plot basis. 100-seed weight was more heritable on an individual plot basis than on a half-sib basis because the numerator in the heritability equation for individual plant selection was σ^2_A and there was complete parental genetic control, whereas for the half-sib families on a plot basis the numerator was only $1/4\sigma^2_A$, and only the genetic contribution of one parent was controlled.

Individual plant heritabilities (Table 10) and the means and variances for selected plants in the gridded isolation planting (Appendix, Table A1), can be used to predict further gains possible through mass selection procedures in IAP1R (Table 11). Because complete data were not available for selected male-sterile plants, and because the mean grain yield of tagged panicles was nearly the same for both family types, only data from the male-fertile panicles were used in the prediction equations. Results of the calculations indicate that the alternating system of gridded mass selection, which is basically S_1 testing without the replicated yield trial phase, would be more efficient for improving these traits than simple gridded mass selection of male-sterile plants. The increased gains per year might, however, be negated over the long term because opportunities for recombination and break-up of linkages

Table 11. Estimated gains from individual plant selection with 20% selection intensity for three traits measured in S_0 plants which gave rise to the families of Experiment I, Ames, 1978 through 1980

Procedure	Traits		
	Grain yield/ main culm panicle	100-seed weight	Seeds/ main culm panicle
	(g)	(g)	
Gridded mass selection of male-sterile plants (1 year/cycle)			
Gain/cycle	0.97	0.12	65
Gain/year	0.97	0.12	65
Estimated gain/year (%)	1.9	5.1	2.9
Alternating gridded mass selection of male-sterile and male-fertile plants (2 years/cycle)			
Gain/cycle	2.9	0.36	195
Gain/year	1.4	0.18	98
Estimated gain/year (%)	2.8	7.7	4.4

would only occur in alternate generations. On the other hand, alternate generations of selfing might be desirable because that procedure would allow better expression of desirable recessive traits (i.e. compact head type, short plant stature, certain disease resistances, etc.). The results indicate mass selection is expected to be an excellent method of increasing seed size. However, it is expected to be less effective for improving seeds/panicle or grain yield.

Family selection (Table 12) is expected to be more effective than mass selection for traits that have low heritability on an individual plant basis. The first two selection procedures described probably are better for a long term recurrent selection program because there is less workload per year than there is with an intensive system such as half-sib family selection (2 years/cycle) or modified ear-to-row (1 year/cycle). Modified ear-to-row selection would be very troublesome in sorghum because segregation for male sterility would occur and the 50% male-fertile plants in each family would have to be rogued from the recombination plantings in order to prevent sib mating. Because families segregate for maturity, this rogueing would require much time and effort. Alternatively, bagged male-sterile plants in each row could be identified and bulk pollinated, which is also labor intensive. S_1 and half-sib family selection, however, require only tagging of plants in the recombination and family formation generations. Data in Table 12 show that S_1 family selection is superior to half-sib family selection when years/cycle is the same. However, a two years/cycle half-sib family testing scheme is reasonable because recombination of selected families and the

Table 12. Estimated gains from family selection with 20% selection intensity for eight traits measured in Experiment I, Ames, 1978 through 1980

Trait	Selection procedures		
	S_1 family selection (3 years/cycle)		
	Estimated gain/cycle	Estimated gain/year	Estimated gain/year (%)
Grain yield (q/ha)	8.8	2.9	4.6
Seeds/panicle	237	79	5.6
100-seed weight (g)	0.35	0.12	4.2
Panicles/plant	0.13	0.04	3.1
Grain yield/panicle (g)	5.6	1.9	4.9
Grain yield/plant (g)	7.8	2.6	5.1
Panicles/plot	4.2	1.4	2.7
Seeds/plant	303	101	5.4

[a]Gain/cycle for HS family selection (2 years/cycle).

[b]Gain/cycle for Modified ear-to-row selection.

Selection procedures					
HS family selection (3 years/cycle)			HS family selection (2 years/cycle) or Modified ear-to-row selection (1 year/cycle)		
Estimated gain/cycle	Estimated gain/year	Estimated gain/year (%)	Estimated gain/cycle	Estimated gain/year	Estimated gain/year (%)
7.2	2.4	3.5	7.2[a]/3.6[b]	3.6	5.3
185	62	4.2	185/92	92	6.3
0.24	0.08	2.8	0.24/0.13	0.13	4.5
0.11	0.04	2.7	0.11/0.06	0.06	4.3
5.1	1.7	4.2	5.1/2.6	2.6	6.2
6.8	2.3	4.1	6.8/3.4	3.4	6.2
3.6	1.2	2.3	3.6/1.8	1.8	3.5
233	78	3.9	233/117	117	5.9

derivation of new families for testing can be accomplished in one generation. The modified ear-to-row system is purported to give the same gains as half-sib family selection (2 years/cycle), but requires more work, so one would choose it only in special circumstances. The 2 years/cycle half-sib family selection scheme is slightly superior to S_1 family selection on a gain per year basis. However, short plant height, early maturity, and certain grain quality traits in grain sorghum are controlled by recessive alleles. Experience has shown that it is difficult to prevent undesirable increases in height and maturity, while maintaining grain quality, under a system of half-sib testing. These traits are more easily controlled by judicious selection of S_1 families.

Some specific recommendations regarding choice of selection methods can be made by using the data in Tables 11 and 12. The only trait for which individual plant selection in a gridded isolation planting is expected to be superior to family selection is 100-seed weight. The alternating gridded mass selection system is recommended for the most rapid improvement of this trait. The IAP1R sorghum population possesses great variability for plant height (75-220 cm) and maturity (60-85 days to midbloom). Recessive alleles for short height and early maturity would tend to be masked in half-sib families, thus making it difficult to develop an improved population of short (100-150 cm), early to medium maturity (65-76 days to midbloom) plants. Therefore, S_1 family selection probably is preferable to half-sib family selection (2 years/cycle) even though estimated gains from selection are slightly lower on a per year

basis. In a practical breeding program, the fact that S_1 family selection requires one-third fewer yield tests than half-sib family selection (2 years/cycle) may outweigh other considerations.

Phenotypic and genetic correlations among grain yield, the primary components of yield, and other agronomic traits in S_1 families (Table 13) are useful because they allow the plant breeder to obtain quantitative measures of interrelationships among traits that may be of value in choosing efficient selection procedures. Due to the large number of paired observations for these correlations, most were significant. The coefficient of determination, r^2 (the coefficient of correlation squared), gives a more accurate picture of the actual relationship. Correlations below 0.50 have coefficients of determination below 25%, meaning that they account for less than one-fourth of the observed variation.

Phenotypic correlations were positive and significant between grain yield and all traits except plants/plot, which showed a small negative correlation with grain yield. However, the only non-grain-yield traits that had correlations with grain yield above ±0.50 were seeds/panicle (0.51), and seeds/plant (0.67). Seeds/panicle was positively correlated with grain yield/panicle, grain yield/plant, plants/plot, and seeds/plant, and had negative correlations with 100-seed weight, panicles/plant, and panicles/plot. However, the only correlations above ±0.50 were 100-seed weight (-0.58), grain yield/panicle (0.71), and seeds/plant (0.81). 100-seed weight was negatively correlated with seeds/plant (-0.51). Panicles/plant was negatively correlated with plants/plot (-0.50), and

Table 13. Phenotypic (above diagonal) and genetic (below diagonal) correlations among traits measured in S_1 families of Experiment I, Ames, 1978 through 1980

	Grain yield	Seeds/ panicle	100-seed weight	Panicles/ plant	Grain yield/ panicle	Grain yield/ plant	Plants/ plot	Panicles/ plot	Seeds/ plant
Grain yield		0.51**	0.18**	0.23**	0.78**	0.94**	-0.17**	0.17**	0.67**
Seeds/panicle	0.53		-0.58**	-0.37**	0.71**	0.45**	0.02	-0.41**	0.81**
100-seed weight	0.22	-0.58		0.15**	0.14*	0.23**	-0.23**	0.05	-0.51**
Panicles/plant	0.27	-0.43	0.22		-0.34**	0.37**	-0.50**	0.88**	0.24**
Grain yield/panicle	0.83	0.72	0.17	-0.35		0.74**	-0.14**	-0.46**	0.53**
Grain yield/plant	0.98	0.47	0.27	0.36	0.79		-0.49**	0.16**	0.70**
Plants/plot	-0.38	0.12	-0.47	-0.58	-0.19	-0.54		-0.03	-0.28**
Panicles/plot	0.16	-0.42	0.07	1.03	-0.42	0.19	-0.25		0.11
Seeds/plant	0.71	0.85	-0.51	0.17	0.58	0.69	-0.16	0.11	

positively correlated with panicles/plot (0.88). Grain yield/panicle was positively correlated with grain yield/plant (0.74), and seeds/plant (0.53). Grain yield/plant was positively correlated with seeds/plant (0.70).

Genetic correlations for S_1 families were very similar in nearly all trait comparisons to the phenotypic correlations. The most unusual value was a genetic correlation of 1.03 for panicles/plot with panicles/plant.

Since the half-sib families came from the same population as the S_1 families, it is not surprising that the correlations among traits in half-sib families (Table 14) were very similar to those for S_1 families (Table 13). But there were several notable differences among traits that were ca. 0.50 or above. Correlations among several traits were somewhat lower for the half-sib families than they were for S_1 families. These included the negative correlation between 100-seed weight and seeds/panicle (-0.49), the negative correlation between 100-seed weight and seeds/plant (-0.39), and the positive correlation between seeds/plant and grain yield/panicle (0.49). Conversely some correlations were higher among the half-sib families, e.g., plants/plot and grain yield/plant (-0.63), and panicles/plot with grain yield/panicle (-0.54). Genetic correlations usually were slightly higher than the phenotypic correlations, in keeping with the pattern observed for S_1 families.

The effect of genetic correlations among traits on progress from selection is made clearer when expected correlated responses to selection are calculated (Table 15). The table shows the expected response in

Table 14. Phenotypic (above diagonal) and genetic (below diagonal) correlations among traits measured in half-sib families of Experiment I, Ames, 1978 through 1980

	Grain yield	Seeds/ panicle	100-seed weight	Panicles/ plant	Grain yield/ panicle	Grain yield/ plant	Plants/ plot	Panicles plot	Seeds/ plot
Grain yield		0.50**	0.26**	0.27**	0.74**	0.92**	-0.29**	0.14*	0.71**
Seeds/panicle	0.56		-0.49**	-0.37**	0.72**	0.42**	-0.04	-0.48**	0.73**
100-seed weight	0.32	-0.42		0.13*	0.24**	0.30**	-0.24**	0.03	-0.39**
Panicles/plant	0.26	-0.39	0.17		-0.34**	0.44**	-0.53**	0.86**	0.35**
Grain yield/panicle	0.81	0.75	0.29	-0.31		0.69**	-0.22**	-0.54**	0.49**
Grain yield/plant	0.97	0.48	0.38	0.35	0.77		-0.63**	0.13*	0.75**
Plants/plot	-0.50	-0.07	-0.39	-0.51	-0.34	-0.70		-0.03	-0.45**
Panicles/plot	0.06	-0.51	0.04	0.90	-0.53	0.08	-0.14		0.12*
Seeds/plant	0.77	0.79	-0.32	0.25	0.58	0.76	-0.46	0.07	

unselected traits when S_1 family selection is for grain yield and the three primary components of yield. Responses are reported as percentages of the expected direct response to S_1 family selection for a given trait. For example, when selection is for grain yield, it is expected that seeds/panicle will also increase, and that the increase will be 55.1% of the expected increase when selection is practiced directly for seeds/panicle. Selection for grain yield is expected to result in favorable increases in all other traits. However, if selection is for seeds/panicle, then seed size, panicles/plant, and panicles/plot are expected to decrease, while yield and other traits increase. Selection for 100-seed weight should increase yield, but a reduction is expected in seeds/panicle and seeds/plant. Selection for panicles/plant is expected to increase yield, but seeds/panicle and grain yield/panicle are expected to decrease. In summary, the table shows clearly that it is advantageous to select for yield itself rather than any of the primary yield components.

Experiment II

Seed for Experiment II came from a random sample of the male-fertile plants harvested at Ames in 1977 from the isolation planting of IAP1R(M)C3. Six grams of seed were used to plant each 4.3 m long plot (ca. 58 seeds/m) to attain a final plant population of 9.8 plants/m (3 plants/foot). Seedbed conditions were harsh in some environments and together with poor germination or seedling vigor of some entries inadequate stands were obtained in 61 plots. Among the 120 S_1 lines

Table 15. Experiment I. Correlated responses in other traits when S_1 family selection is for grain yield, seeds/panicle, 100-seed weight, and panicles/plant. Responses are expressed as percentages of the expected gain from S_1 family selection for a given trait

	Unselected traits							
Trait selected	Grain yield	Seeds/ panicle	100-seed weight	Panicles/ plant	Grain yield/ panicle	Grain yield/ plant	Panicles/ plot	Seeds/ plant
Grain yield	100.0	55.1	20.0	33.3	84.1	100.9	17.8	75.9
Seeds/panicle	51.4	100.0	-56.0	-44.0	70.5	46.8	-45.1	86.8
100-seed weight	21.4	-58.6	100.0	22.2	17.1	27.7	7.7	-53.1
Panicles/plant	23.8	-39.3	20.0	100.0	-31.3	32.6	102.0	15.7

planted, 41 had missing data in at least one replicate in one or more environments. One hundred-nineteen S_1 lines were included in the analyses of individual year data and in the combined analyses.

Uneven emergence in the 1981 Ames planting resulted initially in poor stands. However, additional plants emerged following rains three weeks after planting, stands improved, and yields at Ames were good (71.8 q/ha average yield). At Castana in 1981, seedling emergence also was slow and uneven and poor stands resulted. Very dry conditions prevailed during pollination and grain-filling, resulting in low yields (44.9 q/ha average yield). The 1982 Ames environment was favorable for the establishment of good stands. Cool weather in August, September, and October, however, slowed the maturation of grain. Average yield for this test was 63.6 q/ha. The 1982 Castana environment also was favorable for stand establishment, but plants tillered sparingly and the cool conditions slowed growth and limited yield (50.3 q/ha average yield). Means for all traits measured in each environment are presented in the Appendix (Table A6). Analyses of variance of the data from each environment also are included in the Appendix, Tables A7-A10.

The combined analyses of variance presented in Table 16 show that there were highly significant differences among genotypes for all traits measured except plants/plot. The genotype-environment interaction also was highly significant for all traits except plants/plot. There was little variation for plants/plot because of the high seeding rate and the relatively low final plant population. Coefficients of variation for the combined analyses varied from 8% for plants/plot to 22.1% for

Table 16. Mean squares from the combined ANOVA for traits measured in Experiment II, Ames and Castana, 1981-1982

Source of variation	df	Mean squares		
		Grain yield	Seeds/ panicle	100-seed weight
			(x 100)	(x 10)
Environments (Envir.)	3	32022.3	93.9	716.4
Reps/Envir.	4	1024.9	25.4	1.5
Sets/Reps	10	461.1	22.5	22.3
Envir. x Sets/Reps	30	221.5	13.3	8.2
Genotypes/Sets	113	373.9**	39.8**	50.7**
Envir. x Genotypes/Sets	327	101.8**	8.2**	11.4**
Pooled Error	403	56.3	5.2	8.6
C.V. (%)		17.5	22.1	13.0

Mean squares					
Panicles/ plant	Grain yield/ panicle	Grain yield/ plant	Plants/ plot	Panicles/ plot	Seeds/ plant
(x 10)					(x 100)
1175.3	3424.5	29368.2	106.0	14836.4	2118.6
81.6	132.1	2001.2	34.2	306.3	369.9
20.2	122.8	512.2	6.3	169.6	115.3
6.8	81.4	260.6	12.0	39.5	51.7
30.4**	176.5**	407.3**	5.6^{ns}	276.0**	115.6**
7.3**	39.0**	118.0**	5.8^{ns}	66.4**	26.1**
5.2	22.7	66.4	5.8	45.9	15.5
14.8	19.1	18.3	8.0	14.8	21.8

seeds/panicle. Coefficients of variation were large for grain yield (17.5%) and other traits because of many missing values and large genotype-environment interactions.

Least square means for all entries and ranges among genotypes for traits measured in the combined analysis (Table 17) are relatively low for grain yield because of the low average yields at Castana (47.2 q/ha for Castana vs 67.7 q/ha for Ames). However, the Castana environment typifies the conditions under which much of Iowa's grain sorghum is produced. The mean yield of two commercial hybrids, RS610 and RS671, grown in adjacent plots at Castana during 1981 and 1982 was 50.1 q/ha. Corrected for inbreeding depression, lines from the IAP1R(M)C3 population yielded an estimated 99.8% of the hybrids in the Castana environment. For the yields averaged over four environments, lines from the population yielded an estimated 92% of the hybrids. Individual S_1 family means for grain yield ranged from 38.4 q/ha to 70.3 q/ha. Seed size for individual genotypes varied from 1.87 g/100 seeds to 3.36 g/100 seeds, and seeds/panicle ranged from 732 to 1836. The relatively low plant population of 97,200 plants/ha (39,352 plants/A) allowed genotypes to express much of their genetic potential for producing the maximum number of seed-bearing panicles/plant. Even the most sparse tillering family produced 1.5 panicles/plant and one family averaged 2.48 panicles/plant. The large numbers of panicles/plant resulted from a combination of good basal tillering and the additional ability of certain genotypes to produce axillary-tiller panicles after seed had been set on basal-tiller panicles. Seeds/plant ranged from 1245 to 3591, with a mean of 2346.

Table 17. Least square means, maximum and minimum genotype values, and genotype L.S.D.$_{.05}$ for traits measured in the combined ANOVA for Experiment II, Ames and Castana, 1981-1982

Trait	Genotype values			
	Mean	Minimum	Maximum	Genotype L.S.D.$_{.05}$ [a]
Grain yield (q/ha)	57.7 ± 0.7	38.4	70.3	10.3
Seeds/panicle	1298 ± 22	732	1836	292
100-seed weight (g)	2.58 ± 0.01	1.87	3.36	0.34
Panicles/plant	1.83 ± 0.02	1.50	2.48	0.28
Grain yield/panicle (g)	32.8 ± 0.5	19.8	42.2	6.4
Grain yield/plant (g)	59.4 ± 0.7	39.9	75.3	11.1
Plants/plot	30.1 ± 0.1	26.4	32.8	--
Panicles/plot	55.1 ± 0.6	45.6	75.6	8.3
Seeds/plant	2346 ± 37	1245	3591	521

[a]Difference in genotype means for significance at 0.05 probability level.

Despite the high planting rate the ratio of seeds produced:seeds planted was 280:1.

The data presented in Table 18 show that error variances for the different traits were relatively large. Error variances were larger than the estimates of genotype-environment interaction and genetic variance for all traits, and larger than the phenotypic variance for most traits. The estimate of genotype-environment interaction variance for plants/plot was negative, and the value was the same as the estimate of genetic variance for that trait. The other traits had estimates of genotype-environment interaction variance that ranged from 28% of their genetic variance (100-seed weight) to 70% (grain yield/plant). Grain yield traits displayed the largest ratios of $\hat{\sigma}^2_{ge}/\hat{\sigma}^2_{g}$.

The ratio of $\hat{\sigma}^2_{g}/\hat{\sigma}^2_{ph}$ for each trait provided estimates of heritability on a progeny mean or plot basis (Table 19). Heritabilities on an individual plant basis also were calculated by using the parent-offspring regression method for those traits that were measured on individual plants in the 1977 gridded isolation planting. Plants/plot was not a heritable trait in these environments because of the pronounced over-seeding, and low final plant population. On a progeny mean basis the estimates of heritability were quite high. Seeds/panicle (0.80) was the most heritable trait and grain yield/plant (0.72) was the least. Generally, grain yield traits were the least heritable, and estimates for the other traits were similar. The same general pattern was expressed by heritabilities on a plot basis, which ranged from 0.29 for grain yield/plant to 0.38 for seeds/panicle. Individual plant herita-

Table 18. Estimates of variance components for traits measured in Experiment II, Ames and Castana, 1981-1982

Trait	Variance component			
	σ^2	σ^2_{ge}	σ^2_g	σ^2_{ph}
Grain yield (q/ha)	56.31 ± 3.96	23.86 ± 4.66	36.33 ± 6.69	49.33 ± 7.23
Seeds/panicle (x 100)	5.2 ± 0.4	1.6 ± 0.4	4.2 ± 0.7	5.3 ± 0.7
100-seed weight (x 10) (g)	8.6 ± 0.6	1.5 ± 0.5	5.3 ± 0.9	6.7 ± 0.9
Panicles/plant (x 10)	5.2 ± 0.4	1.1 ± 0.4	3.1 ± 0.5	4.0 ± 1.0
Grain yield/panicle (g)	22.73 ± 1.60	8.66 ± 1.80	18.37 ± 3.15	23.38 ± 3.34
Grain yield/plant (g)	66.41 ± 4.67	27.09 ± 5.42	38.61 ± 7.30	53.68 ± 7.90
Plants/plot	5.82 ± 0.41	-0.02 ± 0.32	-0.02 ± 0.12	0.70 ± 0.09
Panicles/plot	45.92 ± 3.23	10.76 ± 3.20	28.03 ± 4.93	36.46 ± 5.12
Seeds/plant (x 100)	15.5 ± 1.1	5.6 ± 1.2	12.0 ± 2.1	15.3 ± 2.2

bilities were very low for grain yield (0.06), low for seeds/panicle (0.23), and moderate for 100-seed weight (0.43). The fact that the estimate for 100-seed weight on an individual plant basis was higher than the estimate on a plot basis attests to the value of gridded mass selection in reducing spurious environmental variation.

Table 19. Estimates of heritability for traits measured in Experiment II, Ames and Castana, 1981-1982

Trait	Heritability		
	Progeny mean basis	Plot basis	Individual plant basis
Grain yield/unit area	0.74 ± 0.14	0.31 ± 0.06	0.06 ± 0.07
Seeds/panicle	0.80 ± 0.13	0.38 ± 0.06	0.23 ± 0.04
100-seed weight	0.78 ± 0.13	0.34 ± 0.06	0.43 ± 0.05
Panicles/plant	0.77 ± 0.13	0.33 ± 0.06	---
Grain yield/panicle	0.79 ± 0.13	0.37 ± 0.06	---
Grain yield/plant	0.72 ± 0.14	0.29 ± 0.06	---
Plants/plot	0.00	0.00	---
Panicles/plot	0.77 ± 0.14	0.33 ± 0.06	---
Seeds/plant	0.78 ± 0.13	0.36 ± 0.06	---

Estimated gains from individual plant selection in a gridded isolation planting are shown in Table 20. The values were calculated by using the estimates of heritability on an individual plant basis (Table 19) and the data from individual fertile plants harvested from the 1977 isolation planting (Appendix, Table A1). The estimates indicate that gridded mass selection of male-sterile plants at Ames, with testing at

Table 20. Estimated gains from individual plant selection with 20% selection intensity for three traits measured in S_0 plants which gave rise to the families of Experiment II, Ames and Castana, 1981-1982

Procedure	Traits		
	Grain yield/ main culm panicle	100-seed weight	Seeds/ main culm panicle
	(g)	(g)	
Gridded mass selection of male-sterile plants (1 year/cycle)			
Gain/cycle	0.37	0.11	73
Gain/year	0.37	0.11	73
Estimated gain/year (%)	0.6	4.7	2.9
Alternating gridded mass selection of male-sterile and male-fertile plants (2 years/cycle)			
Gain/cycle	1.1	0.34	220
Gain/year	0.6	0.17	110
Estimated gain/year (%)	0.9	7.1	4.4

Ames and Castana, would result in little gain (0.6%/year) in mean grain yield over both environments. Improvement for seeds/panicle was somewhat better (2.9%/year), while the greatest gain was for seed size (4.7%/year). Gridded mass selection with alternate male-sterile and male-fertile plants resulted in higher estimated rates of gain/year for all traits.

Estimates of gains from S_1 family recurrent selection (Table 21) were calculated by using the estimates of variance components (Table 18), heritabilities (Table 19), and least square means (Table 17). Estimated gains/year based on three-years/cycle ranged from 3.7% for 100-seed weight to 6.6% for seeds/panicle. Grain yield was estimated to improve 7.3 q/ha after one cycle, and at a rate of 4.2% per year.

Table 21. Estimated gains from S_1 family selection with 20% selection intensity for selected traits measured in Experiment II, Ames and Castana, 1981-1982

	Selection procedure		
	S_1 family selection (3 years/cycle)		
Trait	Estimated gain/cycle	Estimated gain/year	Estimated gain/year (%)
Grain yield (q/ha)	7.3	2.4	4.2
Seeds/panicle	257	86	6.6
100-seed weight (g)	0.28	0.09	3.7
Panicles/plant	0.21	0.07	3.8
Grain yield/panicle (g)	5.3	1.8	5.4
Grain yield/plant (g)	7.4	2.5	4.1
Panicles/plot	6.5	2.2	3.9
Seeds/plant	427	142	6.1

Comparisons of the estimated gains from individual plant selection in gridded isolation plantings at Ames (Table 20) and from S_1 family testing at Ames and Castana (Table 21) seem relevant. Based on estimated percentage gains/year, gridded mass selection at Ames was better for improving seed size, but S_1 family testing at both environments was superior for the other traits. Fewer resources are required for gridded mass selection at Ames vs S_1 family testing in both environments. Low individual plant heritabilities and considerable genotype-environment interaction for all traits except 100-seed weight, however, make multi-location S_1 testing necessary for maximum gains in population improvement.

Correlations among the nine traits measured in S_1 families are presented (Table 22) for the data recorded in all environments, and for two traits, plant height and days to midbloom, which were measured only at Ames in 1982. Because the latter two traits are highly heritable and little genotype-environment interaction would be expected, they are presented in conjunction with traits measured over several environments. One should use caution when interpreting these correlations, however, because they were calculated from data obtained in a single environment.

Correlations as low as 0.08 were significant, statistically, but attention will be directed mainly to those with coefficients near 0.5. Among the phenotypic correlations grain yield was correlated with seeds/panicle (0.62), grain yield/panicle (0.70), grain yield/plant (0.97), seeds/plant (0.78), and plant height (0.41). Seeds/panicle was

Table 22. Phenotypic (above diagonal) and genetic (below diagonal) correlations among traits measured in S_1 families, Experiment II, Ames and Castana, 1981-1982

	Traits				
	Grain yield	Seeds/ panicle	100 seed weight	Panicles/ plant	Grain yield/ panicle
Grain yield		0.62**	-0.11**	0.14**	0.70**
Seeds/panicle	0.65		-0.58**	-0.43**	0.79**
100-seed weight	-0.16	-0.62		-0.05	0.01
Panicles/plant	0.07	-0.49	-0.05		-0.57**
Grain yield/panicle	0.73	0.80	-0.02	-0.64	
Grain yield/plant	1.004	0.62	-0.09	0.06	0.74
Plants/plot[a]	--	--	--	--	--
Panicles/plot	0.08	-0.44	-0.13	0.999	-0.63
Seeds/plant	0.80	0.83	-0.71	0.08	0.52
Plant height[b]					
Days to midbloom[b]					

[a]Because the heritability of plants/plot was zero, no genetic correlations could be calculated.

[b]Traits measured at Ames, 1982 only.

Traits					
Grain yield/ plant	Plants/ plot	Panicles/ plot	Seeds/ plant	Plant height[b]	Days to midbloom[b]
0.97**	0.12**	0.17**	0.78**	0.41**	0.29**
0.59**	0.14**	-0.40**	0.81**	-0.03	0.35**
-0.05	-0.21**	-0.11**	-0.67**	0.26**	-0.22*
0.16**	-0.15**	0.96**	0.15**	0.16	-0.06
0.71**	-0.003	-0.57**	0.50**	0.26**	0.26**
	-0.11**	0.13**	0.76**	0.45**	0.26**
--		0.12**	0.08*	0.13	0.07
0.07	--		0.17**	0.11	-0.03
0.75	--	0.14		0.08	0.36**
					-0.01

correlated negatively with 100-seed weight (-0.58), and positively with grain yield/panicle (0.79), grain yield/plant (0.59), seeds/plant (0.81), and days to midbloom (0.35). The only sizeable coefficient for 100-seed weight was for the negative association with seeds/plant (-0.67). Panicles/plant was correlated negatively with grain yield/panicle (-0.57), and positively with panicles/plot (0.96). Grain yield/panicle was correlated negatively with panicles/plot (-0.57), and positively with grain yield/plant (0.71) and seeds/plant (0.50). Grain yield/plant was correlated positively with seeds/plant (0.76) and plant height (0.45).

No genetic correlations between plants/plot and other traits are listed in Table 22 because plants/plot was found not to be heritable under the conditions of this experiment. The genetic correlation between grain yield and grain yield/plant was unusually high (1.004). Genetic correlations generally had the same sign as their corresponding phenotypic correlations. There were some exceptions among the coefficients near zero (e.g., -0.02 and 0.01 for 100-seed weight with grain yield/panicle), and in these instances the genetic correlation usually was slightly greater.

Correlated responses in other traits when selection is for grain yield or one of the primary components of grain yield are largely a function of genetic correlations among the traits. The responses given in Table 23 indicate that when S_1 family selection is practiced for grain yield alone, there will be concomitant increases in all traits except 100-seed weight. Seed weight would be expected to decrease by

Table 23. Experiment II. Correlated responses in other traits when S_1 family selection is for grain yield, seeds/panicle, 100-seed weight, and panicles/plant. Responses are expressed as percentages of the expected gain from S_1 family selection for a given trait

Trait selected	Unselected traits							
	Grain yield	Seeds/ panicle	100 seed weight	Panicles/ plant	Grain yield/ panicle	Grain yield/ plant	Panicles/ plot	Seeds/ plant
Grain yield	100.0	62.8	-14.3	6.7	70.2	101.7	7.5	78.4
Seeds/panicle	67.5	100.0	-61.9	-46.7	79.8	64.8	-44.5	84.3
100-seed weight	-16.9	-61.3	100.0	-6.7	-1.8	-9.8	-12.7	-71.9
Panicles/plant	6.7	-47.7	-4.8	100.0	-62.8	5.9	99.8	7.8

an amount that is 14% of the expected gain for 100-seed weight when S_1 family selection is practiced for 100-seed weight alone. It is interesting to note that selection for grain yield/unit area is expected to increase grain yield/plant more than would direct selection for grain yield/plant. If S_1 family selection was practiced for the primary yield component seeds/panicle, then 100-seed weight, panicles/plant, and panicles/plot would decrease while all other traits including grain yield would show gains. Selection for 100-seed weight is expected to result in decreases for all other traits, including a decrease in grain yield which is equivalent to 16.9% of the expected gain from selection for grain yield alone. If one selects for improved tillering ability (panicles/plant), then seeds/panicle, 100-seed weight, and grain yield/panicle should decrease, while all other traits would increase. However, only a small increase in yield is expected (6.7% of the gain from selection for grain yield alone). Table 23 shows clearly that the best method of population improvement should be selection for yield alone. If one were to choose among the primary yield components, then seeds/panicle would be preferred because it should provide the best gains in yield/unit area. Besides being theoretically inefficient, selection for a yield component is not desirable practically because it is much easier to select directly for yield alone. Selection for a yield component requires more work because numbers of plants/plot, panicles/plot, and 100-seed weights must be determined and recorded, as opposed to a simple weighing of grain harvested from each plot for a direct measure of yield.

Experiment III

Experiment III consisted of an unreplicated planting of remnant seed of 14 of the 20 highest yielding S_1 families identified in Experiment I. A commercial hybrid, RS610, was included in the experiment for comparison. Measurements were made on ten spaced plants per S_1 family, and on ten spaced plants of RS610. However, there were only seven competitive spaced plants for Entry 14 because of poor stand establishment.

The mean grain yield/plant over all S_1 lines (Table 24) was slightly higher than the yield for RS610 (107.1 vs 105.7 g). Individual S_1 lines averaged as low as 65.5 g/plant and as high as 131.4 g/plant. Male-fertile segregates in S_1 lines had mean yields that were higher than those of male-sterile plants (112.1 vs 97.2 g/plant). Male-fertile plants also produced more seeds/panicle (1721 vs 1473) and were slightly taller, earlier, and had smaller seed than did the male-sterile plants. There were few (12) plants with compact panicle type and they yielded considerably less than average. Plants with semi-compact and open panicle type yielded about the same (110.9 vs 108.2 g/plant). The compact panicle plants were lower yielding because they had decidedly lower numbers of seeds/panicle, and they were shorter than average.

Plants in the S_1 lines averaged fewer seeds/panicle than the hybrid (1638 vs 1813), larger seeds (2.42 vs 2.23 g), had about the same tillering ability, and were taller (144 vs 127 cm) and later in maturity (75 vs 70 days to midbloom). The short, high-yielding, medium maturity S_1 lines (Entries 14, 6, and 7) all displayed high tillering ability. Numbers of seeds/panicle for Entries 14 and 17 were higher

Table 24. Mean values for traits measured in Experiment III, Ames, 1982

Group	Trait means					
	Grain yield/ plant	Seeds/ panicle	100-seed weight	Panicles/ plant	Plant height	Days to midbloom
	g		g		cm	
14 S_1 lines	107.1	1638	2.42	2.69	144	75
91 male-fertile plants	112.1	1721	2.38	2.73	149	74
46 male-sterile plants	97.2	1473	2.49	2.61	135	76
12 compact panicle plants	91.0	1177	2.44	2.58	131	75
23 semi-compact panicle plants	110.9	1792	2.53	2.48	151	78
107 open panicle plants	108.2	1659	2.38	2.74	144	74
S_1 genotype ranges	65.6-131.4	1236-2127	1.73-2.77	2.30-3.20	112-174	67-81
High-yielding short, medium maturity S_1 lines						
Entry 14	131.4	1842	2.37	2.86	126	75
Entry 6	130.4	1539	2.48	3.00	145	72
Entry 17	126.7	1932	2.16	2.90	149	68
Hybrid check RS610	105.7	1813	2.23	2.67	127	70
119 random S_1 lines	--	--	2.53	--	152	68

than the hybrid, and the seed of Entries 6 and 14 was larger than that of the hybrid. Entries 14 and 6 were later than the hybrid but were within the maturity range acceptable for restorer lines under Iowa conditions.

As a group, the 14 high-yielding S_1 lines selected on the basis of yield alone had slightly smaller seed than the random sample of 119 S_1 lines (2.42 vs 2.53 g), were a little shorter (144 vs 152 cm), and were considerably later in maturity (75 vs 68 days to midbloom). The shift in maturity was not surprising because IAP1R(M) is too early to take full advantage of the growing season in many years at Ames, Iowa.

An unanswered question concerns the combining ability of the 14 high-yielding S_1 lines in hybrid combinations. Yield trials of crosses between short, male-fertile plants from the selected S_1 lines crossed with two A-lines, Combine Kafir 60 and Redbine 58, were planted in 1983 and will provide information to that end. Plants that were crossed in 1982 also were selfed, and an S_2 line of the male parent of each cross was grown in 1983. Because the results of that early generation test of combining ability are outside the scope of this dissertation, one can only speculate on the results at this time. It seems that the combining ability of these lines should be better than that of random lines from the population. It is also anticipated that some experimental hybrids produced by these lines will yield above the RS610 check, because some of the male parents did so as S_1 lines.

DISCUSSION

The data and results of Experiments I, II, and III provide a rather complete description of the breeding value of IAP1R(M)C3. Three hundred twenty-two randomly chosen families were yield tested; 102 half-sib families and 220 S_1 families. Tests were conducted in seven environments over a span of five years.

Population means and genotype ranges were presented in Tables 6 and 17, and Experiment II environment means in Table A6. The weighted mean grain yield of S_1 families grown at Ames (Experiment I and II) was much higher than at Castana (Experiment II), 65.7 vs 47.2 q/ha. The 39% higher yields at Ames were the result of greater moisture availability, less heat stress, and a more fertile soil. In Experiment II, population mean grain yield at Ames was 43% greater (67.7 vs 47.2 q/ha), seeds/panicle was 3% greater (1314 vs 1274), seeds/plant was 27% greater (2618 vs 2056), 100-seed weight was 8% greater (2.68 vs 2.47 g), and panicles/plant was 24% greater (2.03 vs 1.64). Therefore, the mechanism by which genotypes in this population responded to take advantage of favorable environments was primarily by increasing numbers of seeds/plant. This was accomplished largely through increases in panicles/plant. 100-seed weight and seeds/panicle contributed relatively little to increased grain yields in favorable environments.

The population mean grain yield in Experiment II, expressed as a percentage of the grain yield of commercial hybrids RS610 and RS671, was 99.8% at Castana and 86% at Ames. The population performed relatively better in the lower yield environment. This is likely the result of its

earliness which allowed it to partially escape the effects of diminishing soil moisture in late summer. In contrast, Kofoid et al. (1978) tested four Nebraska sorghum random-mating populations in four environments and found that the populations performed better relative to check hybrids in favorable environments. The mean population grain yield in all environments was 94.9% of that of the hybrid checks, compared to a comparable estimate of 92% for IAP1R in Experiment II.

The combined analyses of variance for Experiments I and II (Tables 5 and 16) show that there was highly significant variability present in the population for all traits measured except plants/plot. Variability for this trait was not significant in Experiment II, and highly significant and significant for half-sib and S_1 families, respectively, in Experiment I. Genetic differences in germination and seedling emergence abilities, if present, were not generally well expressed as a consequence of the high rate of seeding relative to the desired plant population. There were no significant genotype-environment interactions for the trait grain yield/unit area for either family type grown at Ames. However, the genotype-environment interaction for grain yield/unit area and all other traits except plants/plot was highly significant for the S_1 families in Experiment II. In Experiment I, the more homozygous S_1 families had larger genotype-environment interactions than the half-sib families for the traits seeds/panicle, panicles/plot, panicles/plant, seeds/plant, 100-seed weight, grain yield/panicle, and grain yield/plant. Coefficients of variation were higher for S_1 than half-sib families in Experiment I, and the coefficients of variation for all traits except

plants/plot were greater in Experiment II than in Experiment I. High coefficients of variation in Experiment II may be ascribed to large genotype-environment interactions and unfavorable growing conditions in several environments. The coefficient of variation was lower in Experiment II for plants/plot because the final plant population was lower than in Experiment I, but the rate of seeding remained the same.

Although estimates of dominance variance were not obtained, it was possible to estimate the degree of non-additive gene action indirectly for traits measured in Experiment I by comparing S_1 and half-sib family means (Table 7). Non-additivity, as measured by estimated inbreeding depression from S_0 to S_∞ (100% homozygosity), was greatest for grain yield traits (-13.7% average) and traits involving numbers of seeds (-8.2% average). Non-additive gene action was less important for seed size (-4.9%), and of little importance for panicles/plant, plants/plot, or panicles/plot. These estimates are consistent with estimates obtained from other grain sorghum random-mating populations. Jan-orn et al. (1976) obtained estimates of dominance and additive variances for nine traits in NP3R. The ratio $\hat{\sigma}^2_D/\hat{\sigma}^2_A$ was greater than unity only for the traits grain yield/unit area (1.38) and seeds/plant (1.11). Bittinger et al. (1981) measured seven traits (but not seed numbers) in PP9 at Lafayette, Indiana, and found that $\hat{\sigma}^2_D/\hat{\sigma}^2_A$ was greater than one only for the trait grain yield/unit area (1.24). Hallauer and Miranda (1981) reported that random-mating populations of maize had an average estimated inbreeding depression (at 100% homozygosity) of -51% for grain yield. This value is several times the estimate for IAP1R sorghum. The differ-

ence is a result of the different modes of reproduction, primarily cross-pollinated vs primarily self-pollinated. Although high-yielding lines may be extracted from IAP1R, they should be used as pollen parents of F_1 hybrids, rather than as lines per se, in order to capitalize on heterosis for seeds/plant and grain yield/unit area.

The assertion that high-yielding inbred lines may be extracted from IAP1R is supported by the trait means and minimum and maximum genotype values presented in Tables 6 and 17, and by the data on inbreeding depression given in Table 7. Assuming that inbreeding depression for grain yield is a constant 13.6% for all genotypes, then the mean grain yield of a set of random inbreds tested at Ames is estimated to be 58.7 q/ha (93.9 bu/A). The low genotype is estimated to yield 35.1 q/ha (56.1 bu/A), and the high 74.5 q/ha (119.2 bu/A). Estimates for inbred performance at Ames and Castana would be 53.8 q/ha (86 bu/A), 35.8 q/ha (57.3 bu/A), and 65.5 q/ha (104.8 bu/A), respectively, for the mean, low, and high. Corroborative data for these estimates were obtained in Experiment III. The Ames 1982 mean yield of the 14 high-yielding S_1 lines was 68.9 q/ha (110.2 bu/A) compared to 68 q/ha (108.8 bu/A) for RS610, a commercial hybrid. The three highest yielding, short S_1 lines averaged 83.3 q/ha (133.3 bu/A). Estimated yields at homozygosity would be 64.2 q/ha (102.7 bu/A) and 77.6 q/ha (124.2 bu/A), respectively, for the mean of 14 S_1 lines and the mean of the top three S_1 lines. It is unlikely that these yields would be realized in practice because (1) the Ames 1982 environment may have been especially favorable (2) these means are based on only 10 plants/S_1

line and (3) phenotypic selection for short plants with desirable agronomic traits may have a negative effect on grain yield.

Comparison of the estimates of variance components for Experiments I and II (Tables 8 and 18) for the two samples of S_1 families shows that environment had a large effect (assuming the two samples are equally random). Estimates of error variance were greater in Experiment II than in Experiment I for all traits except plants/plot, which was lower as a consequence of the reduced plant population. The estimate of error variance for 100-seed weight increased only 2.4% in Experiment II. Estimates of genotype-environment variance were much higher in Experiment II for all traits except plants/plot. There was a tremendous increase in the estimate of genotype-environment variance for grain yield (23.86 vs 1.92).

Estimates of S_1 family genetic variance decreased for some traits in Experiment II because of large genotype-environment interactions. However, the lower plant population in Experiment II allowed greater expression of genetic variance for the traits panicles/plant, panicles/plot, grain yield/plant, seeds/panicle, and seeds/plant. The estimate of S_1 family genetic variance for grain yield decreased 22.6% in Experiment II (36.33 vs 46.97). The estimate of S_1 family genetic variance for grain yield in Experiment I (46.97) is larger than the estimate of 39.9 reported for NP3R (Jan-orn et al., 1976), but much lower than the estimates obtained by Eckebil et al. (1977) of 71.3, 156.2, and 51.6 for NP3R, NP5R, and NP7BR, respectively. The IAP1R estimate from Experiment II (36.33) also seems relatively low. Reasons for the low estimates may

be (1) possible errors in determination of pollen fertility in S_0 plants (2) large genotype-environment interactions in Experiment II and (3) unbagged fertile S_0 plants produced S_1 families that were less homozygous than expected.

The estimate of half-sib family genetic variance obtained for grain yield in Experiment I (31.71) is much larger than the estimate of 12.73 reported for NP3R (Jan-orn et al., 1976). Bittinger et al. (1981) obtained an estimate of half-sib family variance of 18.84 in PP9 using a Design I mating scheme. The higher estimate for IAP1R may be due to (1) great variability in the populations (2) a favorable environment which allowed maximum expression of genetic variance for grain yield (3) possible assortative mating and (4) possible errors in determining pollen fertility in S_0 plants.

Estimates of S_1 family phenotypic variances decreased in Experiment II for the traits grain yield/unit area, 100-seed weight, grain yield/panicle, and plants/plot. The decrease for grain yield/unit area was 10.3%. Variability for plants/plot also decreased dramatically because of the lower plant population established in Experiment II.

The genetic coefficients of variation presented in Table 9 are indicators of the genetic variability in the population relative to the mean. These estimates show clearly that there is a large amount of variability present in IAP1R. Jan-orn et al. (1976) provided data from NP3R from which estimates may be calculated. Comparisons of the coefficients for IAP1R vs NP3R were 16.6 vs 17.2% for grain yield, 20.8 vs 31.4% for seeds/panicle, 14.0 vs 12.5% for seed size, and 14.2 vs

17.3% for panicles/plant. The higher estimates for seeds/panicle and panicles/plant in NP3R are very likely a result of the lower plant population (87,120 vs 123,705 plants/ha) in the Nebraska experiments.

The data from Experiment I concerning estimates of additive genetic variance ($\hat{\sigma}^2_A$) and S_1 family variance ($\hat{\sigma}^2_{S_1}$) presented in Table 9, deviate significantly from theoretical expectations. $\hat{\sigma}^2_A = 4\hat{\sigma}^2_{HS}$ was greater than $\hat{\sigma}^2_{S_1}$ for every trait. Ratios of $\hat{\sigma}^2_A/\hat{\sigma}^2_{S_1}$ ranged from 2.2 for 100-seed weight to 4.8 for plants/plot. The ratio for grain yield/unit area was 2.7.

Jan-orn et al. (1976) reported that $\hat{\sigma}^2_A > \hat{\sigma}^2_{S_1}$ for all traits measured in NP3R grain sorghum random-mating population (the female parent of IAP1R). These scientists produced and then tested 196 half-sib, full sib, and S_1 families in two Nebraska environments. Half-sib families were the progeny of randomly chosen open-pollinated male-sterile plants. S_1 families were derived from random bagged male-fertile plants. The ratio $\hat{\sigma}^2_A/\hat{\sigma}^2_{S_1}$ for grain yield was 1.3. Ratios for other traits ranged from 1.2 for days to midbloom to 3.7 for panicles/plot.

In the absence of epistasis, the genetic expectation for S_1 family variance is $\hat{\sigma}^2_{S_1} = \sigma^2_{A*} + 1/4\sigma^2_D$. They found that the ratio $\hat{\sigma}^2_{A*}/\hat{\sigma}^2_A$ was less than one for all traits, and it was about 0.5 for grain yield traits. The ratio $\hat{\sigma}^2_D/\hat{\sigma}^2_A$ was greater than unity only for grain yield/unit area (1.38) and seeds/plant (1.11). Inexplicably, the ratio for seeds/panicle was -0.05. Jan-orn and co-workers reasoned that $\hat{\sigma}^2_{S_1}$ was low relative to $\hat{\sigma}^2_A$ because (1) $\hat{\sigma}^2_{A*}$ was less than $\hat{\sigma}^2_A$ when frequencies of favorable alleles

were less than 0.5 and dominance and/or epistasis was important and (2) $\hat{\sigma}^2_A$ had been overestimated as a result of assortative mating which occurred when a relatively small number of male-fertile plants of similar height and maturity pollinated male-sterile plants of similar height and maturity. Jan-orn and co-workers stressed the first possibility and downplayed the importance of the second.

The highly unusual environmental conditions which persisted during the period of anthesis in the 1977 isolation planting of IAP1R(M)C3 may have contributed to erroneous estimates of $\hat{\sigma}^2_A$, $\hat{\sigma}^2_{S_1}$, or both. That year anthesis occurred later than usual and during a period of cool, rainy weather. The $\underline{ms}_3$ gene has a relatively stable expression under normal environments. But normal male-fertile ($\underline{Ms}_3\underline{Ms}_3$) sorghum, a crop of tropical origin, may become pollen-sterile under cool conditions (Singh, 1977). Thus some male-fertile plants may have been tagged as male-sterile. Because the male-fertile plants were not bagged, there is the possibility that some may actually have been male-sterile plants tagged incorrectly. And since unbagged male-fertile plants averaged 6% outcrossing, it appears that these S_1 lines would not be as homozygous as S_1 lines produced by bagging.

The possibility that some of the purported half-sib families actually were S_1 families was not investigated. But 18 of the 20 highest yielding purported S_1 families identified in Experiment I were planted for Experiment III. Nineteen of the top 20 purported S_1 families were grown in the 1982 crossing block, where they were bagged. The data on segregation for male-sterility from the breeding nursery and Experiment

III indicated that two and perhaps four of the purported high-yielding S_1 lines might be half-sibs. Therefore, only data for the 14 confirmed S_1 families were presented in Experiment III. These conclusions must be regarded as tentative, however, because there were not sufficient progeny per family to allow a chi-square test for 1:1 vs 3:1 segregation at the 0.05 level of probability. As a result of heterosis for yield, any half-sib families among purported S_1 families would be disproportionately represented in a sample of the highest-yielding S_1 families.

In summary, it appears that the somewhat unusual ratios of $\hat{\sigma}^2_A/\hat{\sigma}^2_{S_1}$ may have been a result of overestimation of $\hat{\sigma}^2_A$ and underestimation of $\hat{\sigma}^2_{S_1}$. Overestimation of $\hat{\sigma}^2_A$ might have been the result of mistakes in tagging (tagging a male-fertile plant as male-sterile) or at harvest, and assortative mating. Assortative mating causes the frequency of homozygotes to be greater than would occur with random mating, thereby, leading to an overestimate of $\hat{\sigma}^2_A$. Underestimation of $\hat{\sigma}^2_{S_1}$ likely resulted because of mistakes in tagging (tagging a male-sterile plant as a male-fertile) or at harvest, and because even true tagged male-fertile plants were partially outcrossed (ca. 6%). Therefore, the S_1 families tested were less homozygous than would be the case when self-pollination was strictly enforced.

Broad sense S_1 family heritabilities (Tables 10 and 19) were higher on a progeny mean basis in Experiment I than in Experiment II for the traits grain yield/unit area, 100-seed weight, grain yield/panicle, grain yield/plant, and plants/plot. They were slightly higher in Experiment II

than in Experiment I for those traits whose expression benefited from the decreased plant population in Experiment II (seeds/panicle, panicles/plant, panicles/plot, and seeds/plant). In Experiment I, heritabilities based on family means were about equal for half-sib and S_1 families for all traits (within one standard error of either estimate). However, it is interesting that estimates for S_1 families were slightly higher for all traits except grain yield/panicle and plants/plot. The shift in ranking for heritability estimates from Experiment I to Experiment II for grain yield/unit area was dramatic. In Experiment I, grain yield/unit area (0.84) and grain yield/panicle (0.84) were most heritable of the nine traits. In Experiment II, only plants/plot (0.00) and grain yield/plant (0.72) had lower estimated heritabilities than grain yield/unit area (0.74). Large genotype-environment interactions for grain yield traits were primarily responsible for the lower estimates for those traits in Experiment II. Relative rankings of the estimates of heritability for the three primary components of grain yield remained generally constant in both experiments. Heritabilities for half-sib families in Experiment I and S_1 families in Experiment II were highest for seeds/panicle, intermediate for 100-seed weight, and lowest for panicles/plot. For S_1 families in Experiment I, 100-seed weight was slightly more heritable than seeds/panicle (0.82 vs 0.79). Heritabilities on a plot basis for S_1 families in the two experiments followed the same general pattern as observed on a progeny mean basis, except that the estimated heritability of seeds/panicle was slightly higher (0.43 vs 0.38) in Experiment I. The estimates of heritability on an individual plant basis were slightly

higher in Experiment II for seeds/panicle (0.23 vs 0.20) and 100-seed weight (0.43 vs 0.41).

Other investigators have reported estimates of heritability in grain sorghum random-mating populations. Jan-orn et al. (1976) calculated estimates of broad sense heritabilities in NP3R for half-sib and S_1 families grown at two Nebraska locations in one year at the same plant population. In harmony with the results for IAP1R in Experiment I, they obtained heritabilities for S_1s that were higher than the estimates for half-sib families for all traits except grain yield/panicle (Jan-orn did not report data for plants/plot). However, their estimates were nearer to those that I obtained in Experiment II. This relationship seems logical because the environments of Experiment II more closely resembled the Nebraska environments. Estimates obtained for IAP1R in Experiment II vs those for NP3R were similar for grain yield/unit area (0.74 vs 0.71), lower for seeds/panicle (0.80 vs 0.88) and seed size (0.78 vs 0.92), and higher for panicles/plant (0.77 vs 0.59). Estimates of individual plant heritabilities for IAP1R, Experiment II vs NP3R were slightly lower for grain yield/unit area (0.06 vs 0.09), much lower for seeds/panicle (0.23 vs 0.40), and similar for seed size (0.43 vs 0.45).

Bittinger et al. (1981) calculated heritabilities for PP9 based on the proportion of the selection differential estimated to be gained from half-sib family selection when remnant seed of selected families is used for recombination. Estimates were 0.37 for grain yield/unit area and 0.56 for seed weight. Eckebil et al. (1977) reported broad sense heritabilities, determined on a progeny mean basis, for S_1 families of three Nebraska populations tested for two years at one Nebraska location.

Estimates for grain yield/unit area ranged from 0.74-0.87, seed size from 0.86-0.91, and panicles/plant from 0.47-0.61. It seems, therefore, that the estimates for IAP1R are similar to those obtained from the Nebraska experiments, although the estimate for the Iowa population for panicles/plot was slightly higher and the estimate for seed size was slightly lower. The very high estimate of individual plant heritability for seeds/panicle (0.40) in NP3R seems at variance with the IAP1R estimate (0.23), but the difference may be due to the much lower plant populations in the Nebraska experiments.

Gridded mass selection in isolation plantings of random-mating populations may prove effective for improving certain traits in grain sorghums. The method is operationally simple, land and labor requirements are not large, and costly yield tests are not required. However, gains may be slow for traits that have low heritability on an individual plant basis, and genotype-environment interactions may make selection at one central station of little value in improving regional performance. Estimates of gains from selection presented in Tables 11 and 20 illustrate these points. Gridded mass selection of male-sterile plants at Ames for grain yield was estimated to result in modest gains/year in performance at Ames (1.9%). But selection at Ames was estimated to be only about one-third as effective (0.6%) when regional adaptibility was tested (Table 20). These results reflect the large genotype-environment interaction for grain yield. The traits 100-seed weight and seeds/panicle did not express such large genotype-environment interactions, and selection at Ames was estimated to allow nearly equal gains in perfor-

mances at Ames and regionally. Projected gains are quite low for grain yield and seeds/panicle, but the estimates for 100-seed weight are sufficiently high to suggest that gridded mass selection would be effective for improving this important agronomic trait. Tables 11 and 20 also indicate that alternating the selection of male-sterile and male-fertile plants should result in substantially greater gains/year. This method improves the efficiency of selection for recessive traits because selfing occurs every other generation. However, opportunities for recombination and breakup of linkage blocks are reduced by one-half. Therefore, gridded mass selection of male-sterile plants seems preferable for long term goals, whereas the alternating system seems better for the short term goals of an applied breeding program.

Family selection procedures (Tables 12 and 21) were estimated to be the best means for improving all traits except 100-seed weight. These methods require costly yield tests, but the frequency of yield testing depends on the method chosen. The modified ear-to-row method requires a yield test every generation, half-sib family testing requires a test every second or third generation, and S_1 family testing every third generation. Modified ear-to-row selection is very labor intensive and cumbersome to use in sorghum populations that are segregating for male sterility. It is difficult to control height, maturity, and grain quality when testing half-sib families. When half-sib family testing is practiced on a two generations/cycle basis opportunities for recombination and breakup of linkages are reduced compared to the three generations/cycle version. Because S_1 family selection was estimated to be

superior to half-sib family testing (three generations/cycle) for nearly all traits, and because the selection of S_1s allows better control of height, maturity and grain quality traits, S_1 testing clearly seems the most desirable method of testing. S_2 testing also would be a good choice, especially in situations where it is desirable that the families in yield tests are more uniform. Estimates of population improvement through S_1 testing indicate that this system would be effective at Ames (Table 12) as well as for a broader area in Iowa (Table 21). The estimates in Table 21 assume multi-location yield trials, which are expensive. If S_1 testing is conducted only at Ames, then improvement in regional performance likely would be less than would be possible with multi-location testing for all traits that display significant genotype-environment interaction (all traits except plants/plot). Theoretically, three cycles of S_1 testing at Ames would produce a population whose mean performance at Ames would surpass that of the mean of two commercial hydrids, RS610 and RS671. But this expectation seems unduly optimistic, because the values used in the prediction equation are based on three years of testing at Ames. In actuality, such a program would more likely rely on information from testing at only one location in one year, and as a consequence genotype-environment interaction could bias the results. However, since the genotype-environment interaction for grain yield was not significant for S_1 families in Experiment I, it seems likely that considerable progress could be made. Similarly, gains for multi-location S_1 testing may be overestimated slightly because in actual practice there would likely be only one year of multi-location testing, not two.

Restrictions on plant height, and especially on maturity, are expected to reduce gains in grain yield. Control of these highly heritable traits should be less difficult with S_1 testing. Judicious choice of male-fertile S_0 plants should suffice to restrain the tendency toward increasing height. In later cycles of S_1 testing, it may be necessary to use dated tags when identifying male-fertile S_0 plants, in order to restrict maturity within desired limits.

Phenotypic and genetic correlations were estimated for nine traits in Experiment I (Tables 13 and 14) and Experiment II (Table 22). Phenotypic and genetic correlations were similar for both family types and both experiments. In addition, phenotypic correlations of plant height and maturity (days to midbloom) with each of the nine traits are presented in Table 22. Genetic correlations among seemingly unrelated traits may be due to pleiotropism or linkage. However, IAP1R(M)C3 was assumed to be at linkage equilibrium.

The results from both experiments indicated that grain yield/unit area was most highly correlated with its "sister traits", grain yield/panicle and grain yield/plant. Genetic correlations among grain yield/unit area and those traits ranged from 0.73-1.004, with the high value occurring in Experiment II where lower plant populations allowed greater expression of individual plant traits. The primary yield component most highly correlated with grain yield/unit area was seeds/panicle (0.53-0.65). Genetic correlations of grain yield with seeds/plant were still higher (0.71-0.80), indicating that genotypes which set large numbers of seeds tended to yield well in all environments. 100-seed weight had

positive genetic correlations with grain yield/unit area in Experiment I (0.22, 0.32), and negative correlations in Experiment II (-0.16). Although the negative correlation is small, it indicates that some large-seeded genotypes yielded poorly in the harsher environments because they tended to set fewer seeds/plant (r_g 100-seed weight, seeds/plant = -0.71), and they could not realize their yield potential when late season heat, drought, or early frosts prevented complete filling of the seed. The primary yield component panicles/plant exhibited small genetic correlations with grain yield/unit area (0.07-0.27).

Phenotypic correlations among height, maturity, and the nine traits (Table 22) are based on data from only one environment (Ames, 1982). Tallness was positively and highly significantly correlated with grain yield/unit area (0.41), grain yield/panicle (0.26), grain yield/plant (0.45), and 100-seed weight (0.26). Lateness was highly significantly correlated with higher grain yield/unit area (0.29), more seeds/panicle (0.35) and seeds/plant (0.36), greater grain yield/panicle and grain yield/plant (both 0.26), and lower 100-seed weight (-0.22). There was no significant correlation between height and maturity (-0.01), which indicates that one should be able to select combine height (100-150 cm) plants of virtually any maturity available in IAP1R. These findings concerning the association of different traits are in close agreement with those reported for NP3R (Jan-orn et al., 1976).

Correlated responses to S_1 selection (Tables 15 and 23) provide valuable estimates concerning the effect of direct selection for grain yield/unit area or the primary components of grain yield on correlated

traits. Data from these tables are useful in evaluating the feasibility of indirect selection for grain yield. Indirect selection for grain yield is expected to be successful if (1) the yield component is more heritable than grain yield (2) there is a substantial positive genetic correlation between the two traits. Results from my experiments indicate that these conditions are not met in IAP1R. My data indicate that the maximum gain in grain yield through indirect selection among yield components occurs when selection is practiced for seeds/panicle (Table 23), but the estimated gain is only 67.5% of that attainable by direct selection for grain yield/unit area. It is encouraging to note that direct S_1 family selection for grain yield/unit area is estimated to simultaneously improve the seven other traits in Experiment I (Table 15), and that selection for yield should improve six of the seven traits measured in Experiment II (Table 23). The slight reduction in 100-seed weight predicted from the data of Experiment II is explained by the fact that some very large-seeded genotypes lack the ability to set large numbers of seeds/plant, which is the most important yield component, especially in harsh environments. The implication is that seed size in IAP1R is not yet optimum for the Ames environment, but may already be higher than optimum for maximum grain yield in the Ames-Castana area. Still, the correlations are low enough not to preclude the possibility of isolating genotypes with high grain yield, high seed numbers, and large seeds.

SUMMARY

The 102 half-sib and 220 S_1 sorghum families evaluated in my experiments were the progeny of randomly chosen male-sterile and male-fertile S_0 plants of IAP1R(M)C3. Three cycles of gridded mass selection for grain weight of selected panicles had been completed in the population. S_0 plants harvested from IAP1R(M)C3 were all of combine height (100-150 cm) and appeared average or better in apparent yielding ability. No selection was imposed for panicle type, seed color, or seed size.

Genotypes were evaluated in replicated experiments at Ames, Iowa from 1978 through 1980 (Experiment I), and at Ames and Castana, Iowa in 1981 and 1982 (Experiment II). Experiment III was a non-replicated observation planting at Ames, Iowa in 1982. Traits evaluated in the replicated experiments were grain yield/unit area, seeds/panicle, 100-seed weight, panicles/plant, grain yield/panicle, grain yield/plant, plants/plot, panicles/plot, and seeds/plant. Two additional traits, plant height and days to midbloom, were evaluated in one environment (Ames) of Experiment II. Additional traits evaluated in Experiment III were pollen fertility and panicle type.

Population means and genotype ranges for the traits indicated that enforced outcrossing in IAP1R had released latent variability through recombination and breakage of linkage blocks without deleterious effects on population means. For example, the population mean grain yield at Ames was 67.9 q/ha, but one genotype yielded only 40.6 q/ha while the best genotype yielded 86.2 q/ha. Expressed as a percentage of the grain yield of two commercial hybrids grown in the same environments, the

population mean grain yield was 72%, and the highest yielding genotype yielded 92%. Means and ranges for the components of yield and for other agronomic traits were large enough to indicate that IAP1R should be a good source population for the extraction of restorer lines. The genetic coefficient of variation was 16.6% for grain yield, and ranged from 5.3% for plants/plot to 20.8% for seeds/panicle.

Estimates of inbreeding depression were significant for grain yield traits, traits that involved seed numbers, and 100-seed weight. Non-additive gene action was estimated to be greatest for the grain yield traits, intermediate for the seed number traits, and lowest for 100-seed weight. All other traits displayed additive gene action. The estimate of inbreeding depression at 100% homozygosity for grain yield/unit area, -13.6%, is quite low compared to a crop such as maize and indicates that inbred lines of considerable vigor could be isolated from IAP1R. Inbreds yielding as high as 74.5 q/ha (119.2 bu/A) at Ames theoretically could be derived from the population. Heterosis for seeds/panicle and grain yield/unit area is considerable, however, suggesting that inbreds from the population would be best used as pollen parents for F_1 hybrids.

Grain yields were much lower in Experiment II because there were several unfavorable environments. The mean grain yield in Experiment II for S_1 families at Ames was 67.7 q/ha, but at Castana it was 47.2 q/ha. Higher yields in the more favorable environments were largely a result of greater numbers of seeds/plant achieved through increases in panicles/plant, rather than increases in 100-seed weight or seeds/panicle. Interestingly, S_1 lines yielded better relative to the commercial

hybrids in the harsher environments (99.8% vs 86%). This is likely a result of the earliness of IAP1R, which allowed S_1 lines to partially escape the effects of diminishing soil moisture in late summer.

Genotype-environment interactions were not significant for either family type in Experiment I for grain yield/unit area or 100-seed weight. However, genotype-environment interactions were highly significant in Experiment II for grain yield/unit area and all major components of grain yield. In Experiment I, estimates of error variance were greater for S_1 families than for half-sib families for grain yield/unit area and grain yield/panicle. Estimates of genetic variance were greater for S_1 families than for half-sib families for all traits except plants/plot, but they were not so great as one would expect based on genetic theory. A likely explanation for the discrepancy is that some S_0 plants were identified incorrectly for pollen fertility or sterility in the 1977 isolation planting of IAP1R(M).

Heritability estimates for S_1 families determined from variance components were much lower for many traits in Experiment II than in Experiment I. This was a result of large genotype-environment interactions and environments that were less favorable for expression of genetic variance in Experiment II. The heritability of grain yield/unit area was 0.74 in Experiment II vs 0.85 in Experiment I, and the comparison for grain yield/plant was 0.72 vs 0.81. Conversely, the estimate for panicles/plant was greater in Experiment II (0.77 vs 0.66), likely a result of the lower plant population in Experiment II. Estimates for the seed number traits and 100-seed weight were similar in the two

experiments. The estimates of individual plant heritability for grain yield/unit area were very low in both experiments (0.06 and 0.13). Individual plant heritabilities for seeds/panicle (0.23, 0.20) and 100-seed weight (0.43, 0.41) were nearly alike in the two experiments.

Estimates of genetic gain from different recurrent selection procedures indicated that gridded mass selection would be very effective for improving seed size, but only marginally useful for improving seeds/panicle and grain yield/unit area. S_1 testing was determined to be the best method for improving all traits other than 100-seed weight. Assuming three years/cycle, the estimated gain for grain yield/unit area was 4.2%/year when S_1 testing was conducted at both Ames and Castana, and population performance was evaluated as the mean of those two locations.

Phenotypic and genetic correlations among traits were similar in magnitude. Among the primary yield components, seeds/panicle showed the highest correlation with grain yield/unit area (genetic correlations of 0.53-0.65). The associated trait seeds/plant had still higher genetic correlations with grain yield/unit area (0.71-0.80). Genetic correlations of 100-seed weight with yield/unit area ranged from 0.32 to -0.16. The negative correlation from Experiment II is small, but it indicates that some very large-seeded genotypes were ill-suited to the less favorable environments. Panicles/plant displayed small genetic correlations with grain yield/unit area (0.07-0.27).

Phenotypic correlations calculated from the 1982 Ames data showed that plant height and maturity were correlated significantly with several

traits. Height was correlated positively with grain yield/unit area (0.41) and 100-seed weight (0.26). Maturity was correlated positively with seeds/panicle (0.35), seeds/plant (0.36), and grain yield/unit area (0.29), but it was correlated negatively with 100-seed weight (-0.22). The plant height with maturity correlation was -0.01, indicating that short genotypes with a range of maturities could be selected from the population.

Correlated responses to S_1 family selection for grain yield and the three primary components of grain yield indicated that indirect selection for grain yield in IAP1R would not be effective. Direct selection for grain yield was estimated to result in concomitant favorable increases in the means for all primary yield components when selection and evaluation are carried out at Ames. When selection and evaluation trials are conducted at Ames and Castana, direct selection for grain yield/unit area was estimated to result in positive increases in the means of all components except 100-seed weight.

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ACKNOWLEDGMENTS

The author wishes to express his sincere gratitude to the following:

The Agronomy Department, Dr. John Pesek, Head, for providing financial assistance in the form of a Graduate Research Assistantship.

Dr. R. E. Atkins for his guidance, assistance, patience, and hospitality throughout the course of my stay in Ames. His contributions to the conduct of the field experiments and preparation of this manuscript are especially greatly appreciated.

Dr. O. S. Smith for his assistance and encouragement in the course of the sometimes difficult and frustrating efforts to analyze data from these experiments. Special thanks for his unending patience and unfailing sense of humor.

Drs. P. N. Hinz, M. D. Simons, and A. R. Hallauer for their advice and assistance.

Dr. P. J. Berger, for statistical advice and Ronnie Silcox, graduate student in Animal Science, for the many hours he spent helping me use the LSML76 computer program.

Fellow graduate students and friends for their encouragement, assistance, and fellowship during my graduate studies at I.S.U.

APPENDIX

Table A1. Means and variances for grain yield, 100-seed weight, and seeds/panicle of the randomly chosen male-sterile and male-fertile plants, from which the HS and S_1 families tested were derived, as grown in the 1977 gridded isolation planting of IAP1R(M)C3

	Trait					
	Grain yield/ main culm panicle		100-seed weight		Seeds/ main culm panicle	
Experiment and family type	Mean	Variance	Mean	Variance	Mean	Variance
	(g)					
Experiment I						
101 male-fertile plants	52.2 ± 1.1	113.39	2.38 ± 0.04	0.1779	2234 ± 46	216125.49
102 male-sterile plants	53.4 ± 1.2	136.12	Data not recorded		---	---
Experiment II						
119 male-fertile plants	59.0 ± 0.8	78.38	2.40 ± 0.04	0.1459	2510 ± 42	206734.66

Table A2. Individual year means for traits measured in Experiment I, Ames, 1978 through 1980

Trait	Mean			
	All entries			Half-sib
	1978	1979	1980	1978
Grain yield (q/ha)	66.1 ± 0.3	67.8 ± 0.3	62.8 ± 0.3	69.2 ± 0.4
Seeds/panicle	1487 ± 10	1578 ± 12	1220 ± 8	1528 ± 16
100-seed weight (g)	2.73 ± 0.02	2.87 ± 0.02	2.90 ± 0.01	2.76 ± 0.02
Panicles/plant	1.40 ± 0.01	1.25 ± 0.01	1.45 ± 0.01	1.43 ± 0.01
Grain yield/ panicle (g)	39.9 ± 0.2	44.6 ± 0.2	34.8 ± 0.2	41.6 ± 0.3
Grain yield/ plant (g)	55.4 ± 0.4	55.1 ± 0.3	50.1 ± 0.3	58.8 ± 0.6
Plants/plot	37.6 ± 0.2	38.3 ± 0.2	39.1 ± 0.2	37.0 ± 0.2
Panicles/plot	51.7 ± 0.3	47.6 ± 0.3	56.5 ± 0.3	52.0 ± 0.4
Seeds/plant	2063 ± 17	1952 ± 15	1749 ± 14	2162 ± 25

Mean				
Half-sib		S_1		
1979	1980	1978	1979	1980
70.5 ± 0.4	63.9 ± 0.3	62.9 ± 0.5	65.1 ± 0.5	61.8 ± 0.4
1606 ± 17	1220 ± 11	1446 ± 13	1550 ± 16	1219 ± 12
2.91 ± 0.02	2.94 ± 0.02	2.70 ± 0.02	2.84 ± 0.02	2.86 ± 0.02
1.26 ± 0.01	1.45 ± 0.01	1.36 ± 0.01	1.24 ± 0.01	1.46 ± 0.01
46.0 ± 0.3	35.4 ± 0.2	38.3 ± 0.3	43.1 ± 0.3	34.2 ± 0.2
57.3 ± 0.4	50.9 ± 0.4	51.8 ± 0.5	52.9 ± 0.4	49.3 ± 0.4
38.4 ± 0.2	39.1 ± 0.2	38.1 ± 0.3	38.3 ± 0.2	39.0 ± 0.2
48.0 ± 0.4	56.4 ± 0.4	51.3 ± 0.3	47.3 ± 0.4	56.6 ± 0.4
1999 ± 22	1751 ± 21	1962 ± 21	1904 ± 22	1747 ± 18

Table A3. Mean squares from the ANOVA for traits measured in Experiment I, Ames, 1978

Source of variation	df	Mean squares		
		Grain yield	Seeds/ panicle	100-seed weight
			(x 100)	(x 10)
Replications (Reps)	1	223.2	0.1	48.0
Sets/Reps	10	227.3	26.9	44.0
Genotypes/Sets	197	156.4**	11.3**	21.7**
S_1/Sets[a]	95	151.9**	12.6**	27.4**
HS/Sets[a]	96	121.8**	9.7**	16.4**
S_1 vs HS/Sets	6	779.9**	16.8**	17.7^{ns}
Error	197	42.9	4.1	8.9
S_1	95	44.5	3.2	8.0
HS	96	39.9	4.9	9.9
All entries C.V. (%)		9.5	13.6	10.9
HS entires C.V. (%)		10.6	12.3	10.8
S_1 entries C.V. (%)		9.1	14.5	11.4

[a]HS = half-sib family; S_1 = S_1 family; as used in this and all subsequent tables.

*,**Indicate significance beyond the 0.05 and 0.01 probability levels, respectively; ns = not significant; as used in this and all subsequent tables.

Mean squares					
Panicles/ plant	Grain yield/ panicle	Grain yield/ plant	Plants/ plot	Panicles/ plot	Seeds/ plant
(x 10)					(x 100)
46.8	72.8	1531.0	217.3	1.0	108.4
41.9	117.6	627.5	63.3	263.5	143.1
8.3**	63.4**	193.1**	19.5**	58.2**	34.1**
7.8**	65.4**	167.4**	22.3**	60.4**	32.7**
7.9**	51.9**	164.8**	15.1^{ns}	55.9**	30.9**
20.2**	216.9**	1052.3**	43.8**	62.7*	106.9**
3.0	14.2	60.0	12.7	23.4	11.5
1.9	14.5	47.8	13.6	17.4	9.2
2.9	13.8	61.2	10.9	24.8	12.5
12.3	9.4	14.0	9.5	9.4	16.4
10.2	9.9	13.3	9.7	8.1	15.4
11.9	8.9	13.3	8.9	9.6	16.4

Table A4. Mean squares from the ANOVA for traits measured in Experiment I, Ames, 1979

Source of variation	df	Mean squares		
		Grain yield	Seeds/ panicle	100-seed weight
			(x 100)	(x 10)
Replications (Reps)	1	473.5	32.8	0.0
Sets/Reps	10	244.9	26.7	21.0
Genotypes/Sets	197	122.5**	12.5**	20.5**
S_1/Sets	95	130.0**	14.3**	23.5**
$\overline{HS}$/Sets	96	86.4**	10.7**	16.9*
S_1 vs HS/Sets	6	580.6**	12.8*	30.3*
Error	197	39.8	5.4	11.5
S_1	95	48.3	5.3	11.0
$\overline{HS}$	96	33.3	5.7	11.7
All entries C.V. (%)		9.3	14.7	11.8
S_1 entries C.V. (%)		10.7	14.8	11.7
HS entries C.V. (%)		8.2	14.8	11.8

Mean squares					
Panicles/ plant	Grain yield/ panicle	Grain yield/ plant	Plants/ plot	Panicles/ plot	Seeds/ plant
(x 10)					(x 100)
11.4	238.0	1249.0	146.6	6.2	166.9
18.1	225.5	152.7	25.4	250.2	21.6
3.8**	66.7**	109.2**	9.6^{ns}	43.6**	19.4**
3.8**	68.9**	100.6**	8.7^{ns}	47.4**	22.3**
3.8**	55.2**	100.2**	10.7^{ns}	38.9^{ns}	15.7*
5.6*	214.0**	391.4**	5.3^{ns}	58.6^{ns}	33.4**
2.3	20.4	38.3	9.9	29.2	9.7
2.3	19.5	39.4	9.4	25.3	9.5
2.2	20.7	37.6	10.5	30.3	9.9
12.1	10.1	11.2	8.2	11.4	16.0
12.3	10.2	11.9	8.0	10.6	16.2
11.7	9.9	10.7	8.4	11.5	15.8

Table A5. Mean squares from the ANOVA for traits measured in Experiment I, Ames, 1980

Source of variation	df	Mean squares		
		Grain yield	Seeds/ panicle	100-seed weight
			(x 100)	(x 10)
Replications (Reps)	1	0.0	25.5	4.7
Sets/Reps	10	123.5	9.2	22.9
Genotypes/Sets	197	117.2**	9.6**	18.9**
S_1/Sets	95	144.0**	12.4**	22.1**
HS/Sets	96	92.2**	6.6**	15.8**
S_1 vs HS/Sets	6	94.4**	11.0**	18.7*
Error	197[a]	30.5	2.6	7.4
S_1	95[a]	39.7	2.8	6.1
HS	96[a]	22.2	2.3	8.4
All entries C.V. (%)		8.8	13.3	9.4
S_1 entries C.V. (%)		10.2	13.7	8.6
HS entries C.V. (%)		7.4	12.5	9.9

[a]Because of missing values, the traits seeds/panicle, panicles/plant, grain yield/panicle, and panicles/plot had 1 degree of freedom less than indicated for S_1 and HS errors, and 2 degrees of freedom less for overall error.

Mean squares					
Panicles/ plant	Grain yield/ panicle	Grain yield/ plant	Plants/ plot	Panicles/ plot	Seeds/ plant
(x 10)					(x 100)
0.0	117.6	256.6	126.9	317.4	47.4
4.9	63.9	107.5	11.1	45.1	17.7
5.4**	53.5**	104.4**	9.9^{ns}	70.6**	15.2**
6.5**	63.3**	125.9**	11.1^{ns}	78.9**	18.7**
4.2**	41.8**	84.9**	9.1^{ns}	58.0**	12.1**
7.7**	86.0**	74.0*	4.6^{ns}	140.4**	9.1^{ns}
2.5	9.8	33.6	9.2	28.5	7.6
2.4	12.2	31.1	8.2	28.0	6.6
2.5	7.5	35.8	10.2	27.6	8.6
10.9	9.0	11.6	7.8	9.4	15.8
10.6	10.2	11.3	7.3	9.4	14.8
10.8	7.7	11.7	8.2	9.3	16.7

Table A6. Individual environment means for traits measured in Experiment II, Ames and Castana, 1981-1982

Trait	Location and year			
	Ames 1981	Castana 1981	Ames 1982	Castana 1982
Grain yield (q/ha)				
Mean	71.8 ± 0.5	44.0 ± 0.7	63.6 ± 0.4	50.3 ± 0.4
L.S. mean[a]	71.9	44.9	63.6	50.3
Seeds/panicle				
Mean	1389 ± 15	1255 ± 19	1239 ± 10	1293 ± 17
L.S. mean[a]	1391	1267	1240	1292
100-seed weight (g)				
Mean	2.83 ± 0.02	2.49 ± 0.02	2.53 ± 0.02	2.45 ± 0.02
L.S. mean[a]	2.83	2.49	2.53	2.45
Panicles/plant				
Mean	1.95 ± 0.02	1.56 ± 0.02	2.10 ± 0.01	1.71 ± 0.01
L.S. mean[a]	1.94	1.57	2.10	1.71
Grain yield/panicle (g)				
Mean	38.7 ± 0.3	30.3 ± 0.5	30.8 ± 0.2	31.0 ± 0.3
L.S. mean[a]	38.7	30.7	30.8	31.0
Grain yield/plant (g)				
Mean	73.9 ± 0.6	47.1 ± 0.8	63.9 ± 0.5	51.7 ± 0.4
L.S. mean[a]	73.9	48.1	63.9	51.7
Plant/plot				
Mean	30.2 ± 0.1	29.3 ± 0.3	30.9 ± 0.1	30.1 ± 0.1
L.S. mean[a]	30.3	29.2	30.8	30.1

Panicles/plot				
Mean	58.7 ± 0.5	45.3 ± 0.5	64.7 ± 0.4	51.4 ± 0.5
L.S. mean[a]	58.7	45.6	64.7	51.4
Seeds/plant				
Mean	2663 ± 26	1955 ± 32	2572 ± 25	2156 ± 24
L.S. mean[a]	2662	1993	2572	2156
Days to midbloom				
Mean	---	---	68 ± 0.1	---
L.S. mean[a]	---	---	68	---
Plant height (cm)				
Mean	---	---	152 ± 0.5	---
L.S. mean[a]	---	---	152	---

[a]Least squares mean, obtained after estimated values have replaced missing values.

Table A7. Mean squares from the ANOVA for traits measured in Experiment II, Ames, 1981

Source of variation	df	Mean squares								
		Grain yield	Seeds/ panicle	100-seed weight	Panicles/ plant	Grain yield/ panicle	Grain yield/ plant	Plants/ plot	Panicles/ plot	Seeds/ plant
			(x 100)	(x 10)	(x 10)					(x 100)
Replications (Reps)	1	3.7	0.3	0.8	3.7	2.5	2.2	0.8	51.2	0.1
Sets/Reps	10	270.9	16.0	9.7	12.5	78.3	434.3	11.9	77.8	103.2
Genotypes/ Sets	111[a]	161.1**	15.4**	21.7**	16.3**	82.3**	186.7**	4.1[ns]	154.4**	53.1**
Error	103[a]	57.0	4.8	6.6	5.9	24.4	68.2	4.7	48.1	14.8
C.V. (%)		10.5	15.8	9.1	12.4	12.8	11.2	7.2	11.8	14.5

[a]There were 113 degrees of freedom for genotypes/sets and error for the trait 100-seed weight. All other traits had missing data.

Table A8. Mean squares from the ANOVA for traits measured in Experiment II, Castana, 1981

Source of variation	df	Mean squares		
		Grain yield	Seeds/ panicle	100-seed weight
			(x 100)	(x 10)
Replications (Reps)	1	5129.9	83.6	15.5
Sets/Reps	10	694.1	31.1	16.4
Genotypes/Sets	103[a]	260.8**	25.7**	24.8**
Error	76[a]	98.7	6.8	11.5
C.V. (%)		22.6	20.7	13.6

[a]There were 113 degrees of freedom for genotypes/sets and error for the trait 100-seed weight. All other traits had missing data.

Mean squares					
Panicles/ plant	Grain yield/ panicle	Grain yield/ plant	Plants/ plot	Panicles/ plot	Seeds/ plant
(x 10)					(x 100)
417.6	485.8	8845.3	76.5	2034.9	1506.4
15.9	227.4	671.5	22.0	87.2	112.0
12.1**	105.0**	304.3**	14.8^{ns}	101.7**	74.1**
5.0	42.8	122.4	15.4	55.2	19.9
14.3	21.6	23.5	13.3	16.4	22.8

Table A9. Mean squares from the ANOVA for traits measured in Experiment II, Ames, 1982

Source of variation	df	Mean squares			
		Grain yield	Seeds/ panicle	100-seed weight	Panicles/ plant
			(x 100)	(x 10)	(x 10)
Replications (Reps)	1	10.2	7.2	10.0	3.8
Sets/Reps	10	59.7	7.0	12.4	5.2
Genotypes/Sets	113	121.9**	9.7**	22.6**	12.2**
Error	112[a]	42.6	2.5	6.1	4.8
C.V. (%)		10.3	12.8	9.7	10.4

[a]There were 113 degrees of freedom for error for the traits 100-seed weight, days to midbloom, and plant height. All other traits had missing data.

Mean squares						
Grain yield/ panicle	Grain yield/ plant	Plants/ plot	Panicles/ plot	Seeds/ plant	Days to midbloom	Plant height
				(x 100)		
14.1	124.2	43.8	72.1	45.3	24.9	403.8
14.1	69.2	5.4	66.6	37.5	10.4	1901.4
40.8**	128.9**	3.4^{ns}	110.8**	33.7**	15.0**	391.0**
7.3	51.2	4.7	34.1	15.2	2.3	55.9
8.8	11.2	7.0	9.0	15.1	2.2	4.9

Table A10. Mean squares from the ANOVA for traits measured in Experiment II, Castana, 1982

Source of variation	df	Mean squares								
		Grain yield	Seeds/ panicle	100-seed weight	Panicles/ plant	Grain yield/ panicle	Grain yield/ plant	Plants/ plot	Panicles/ plot	Seeds/ plant
			(x 100)	(x 10)	(x 10)					(x 100)
Replications (Reps)	1	253.7	15.8	0.0	1.5	86.2	322.1	0.9	5.3	76.6
Sets/Reps	10	44.1	4.2	14.3	7.0	22.3	51.0	0.9	65.2	6.9
Genotypes/ Sets	113	150.4**	15.4**	18.3*	12.4**	72.1**	159.1**	1.4^{ns}	113.0**	37.7**
Error	112[a]	40.7	7.1	12.5	5.1	23.0	42.0	1.5	49.5	13.4
C.V. (%)		12.7	20.7	14.4	13.3	15.5	12.5	4.0	13.7	17.0

[a]There were 113 degrees of freedom for error for the trait 100-seed weight. All other traits had missing data.